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An Analysis of the Ability to Detect Reductions in Year-class Strength of the Hudson River White Perch (*Morone americana*) Population[1,2]

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VAN WINKLE, W., D. S. VAUGHAN, L. W. BARNTHOUSE, AND B. L. KIRK. 1981. An analysis of the ability to detect reductions in year-class strength of the Hudson River white perch (*Morone americana*) population. Can. J. Fish. Aquat. Sci. 38: 627–632.

Impingement rates for young-of-the-year white perch (*Morone americana*) in the Hudson River were analyzed to address two questions: (1) assuming a specified number of years of additional data, what is the minimum fractional reduction in mean year-class strength that could be detected, and (2) assuming a specified fractional reduction in mean year-class strength, how many additional years of impingement data would be required to detect the reduction. Our results indicate that the variability in the baseline data is so great that 10 more years of data are not adequate for detecting even substantial (>50%) reductions in mean year-class strength and that more than 50 years of data would be required to detect an actual 50% reduction in mean year-class strength, given a Type II error of 50%. Our methodology offers a generic tool for establishing bounds on reductions in fish stocks and for estimating the number of additional years of data required to detect such reductions.

Key words: fractional reduction, impingement, power plant, statistical power, Type I and Type II errors, white perch, year-class strength

VAN WINKLE, W., D. S. VAUGHAN, L. W. BARNTHOUSE, AND B. L. KIRK. 1981. An analysis of the ability to detect reductions in year-class strength of the Hudson River white perch (*Morone americana*) population. Can. J. Fish. Aquat. Sci. 38: 627–632.

Nous avons analysé les taux d'empiètement de bars-perches de l'année dans le fleuve Hudson dans le but de trouver réponse à deux questions : (1) en supposant des données supplémentaires pour un nombre spécifié d'années, quelle est la diminution fractionnelle minimale d'abondance moyenne d'une classe d'âge qu'il serait possible de détecter, et (2) en

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supposant une diminution fractionnelle spécifiée d'abondance moyenne d'une classe d'âge, combien faudrait-il d'années supplémentaires de données sur l'empiètement pour pouvoir détecter la diminution. D'après nos résultats, la variabilité des données de base est tellement grande que 10 années supplémentaires de données ne suffisent pas à détecter même des diminutions importantes (>50%) d'abondance moyenne des classes d'âge, et il faudrait plus de 50 ans de données pour détecter une diminution réelle de 50% d'abondance moyenne des classes d'âge, avec une erreur de type II de 50%. Notre méthodologie permet d'établir des limites à la réduction des stocks de poissons et d'estimer le nombre d'années supplémentaires de collection de données nécessaires à la détection de telles diminutions.

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FISHERIES managers and other decision makers frequently must predict the probable reduction in the size of a fish stock or in the strength of year-classes prior to the imposition of a new or additional impact on the population. Although it may not be possible to address the problem directly with the degree of certainty desirable, it is possible to estimate what reductions could be detected using standard statistical techniques if a historical time series of stock sizes or year-class strengths is available.

White perch (*Morone americana*) is one of the dominant fish species in the Hudson River. It has been the subject of intense study since 1972 with respect to potential population-level effects of entrainment and impingement mortality at power plants (Barnthouse et al. 1981; Boreman et al. 1981). As part of U.S. Environmental Protection Agency hearings, we performed a detailed evaluation of impingement losses of white perch at five power plants on the Hudson River (Van Winkle et al. 1980). In this evaluation we used impingement rate of young-of-the-year white perch, especially at the large downriver power plants in winter where most young-of-the-year overwinter, as an approximate index of year-class strength. We concluded, based on regression analyses of impingement rate of young-of-the-year white perch versus year, that there was no statistically significant change in year-class strength during the period 1972 through 1977. Thus, we used impingement rates for 1972 through 1977 at these five power plants as baseline data to provide a measure of "natural" variability in year-class strength. The two questions addressed in this paper are:

1) Based on a given number of years of additional impingement data (starting in 1978), what is the minimum fractional reduction in mean year-class strength of white perch in the Hudson River one could expect to detect?
2) Given that we want to be able to detect a specified fractional reduction in mean year-class strength (e.g. a 25 or 50% reduction), how many additional years of impingement data (starting in 1978) would be required?

Obviously these two questions are related. For the first question fractional reduction is the dependent variable and number of additional years of impingement data is the independent variable, and for the second question the two variables are reversed. However, the two questions merit separate answers because they represent different points of view on monitoring and managing the Hudson River white perch population in years to come. For both questions we are postulating that no reduction in mean year-class strength due to impingement or other causes occurred before 1978, but that some reduction in mean year-class strength due to impingement may occur starting in 1978.

Methods and Data Base

To study the relationship between power of a statistical test and sample size, it is first necessary to specify the null and alternative hypotheses. Our null hypothesis is that there is no difference between the population means underlying the two samples, i.e.

$$(1) \quad H_0: \mu_1 = \mu_2,$$

where μ_1 is mean year-class strength for young-of-the-year white perch in the Hudson River before 1978, and μ_2 is mean year-class strengh for 1978 and later years. The alternative hypothesis is:

$$(2) \quad H_A: \mu_1 > \mu_2.$$

In other words, H_A is one-tailed and includes those cases where there is a reduction in mean year-class strength for 1978 and later years relative to that before 1978.

If we assume a normal distribution underlying each of the two samples of indices of year-class strength, as well as a homogeneous underlying variance, then the appropriate test statistic for the difference between the two sample means is given by

$$(3) \quad t = \frac{\bar{X}_1 - \bar{X}_2}{\sqrt{s_p^2\,(1/n_1 + 1/n_2)}},$$

where the subscripts denote the two samples; $\bar{X}_1$ and $\bar{X}_2$ are the sample means; n_1 and n_2 are the sample sizes (i.e. number of years, since only one index of year-class strength is obtained each year); and s_p^2 is the pooled variance:

$$(4) \quad s_p^2 = \frac{(n_1 - 1)s_1^2\,(n_2 - 1)s_2^2}{n_1 + n_2 - 2},$$

where s_1^2 and s_2^2 are the sample variances (Sokal and Rohlf 1969). This test statistic is distributed as a central t-distribution with $\nu = (n_1 + n_2 - 2)$ degrees of freedom. The null hypothesis is rejected when the calculated t (or test statistic) is greater than the one-tailed tabled value for $t_{\nu,\alpha}$.

Thus, under the null hypothesis (H_0: $\mu_1 - \mu_2 = 0$),

$$(5)\quad \Pr\{t > t_{\nu,\alpha}\} = \alpha,$$

where Pr { } indicates the probability of occurrence for the event within the braces. Also, under the alternative hypothesis (H_A: $\mu_1 - \mu_2 > 0$), the difference between means is positive such that

$$(6)\quad \Pr\{t > t_{\nu,\alpha}\} = 1 - \beta,$$

where β is the probability of accepting the null hypothesis when it is false. The power of a statistical test ($1 - \beta$) is the probability of correctly rejecting the null hypothesis.

Under the alternative hypothesis the test statistic t is no longer distributed as a central t-distribution. Subtracting (3) from each of the two terms within the braces of (6), we obtain

$$(7)\quad \left\{ t - \frac{\bar{X}_1 - \bar{X}_2}{\sqrt{s_p^2\,(1/n_1 + 1/n_2)}} > t_{\nu,\alpha} - \frac{\bar{X}_1 - \bar{X}_2}{\sqrt{s_p^2\,(1/n_1 + 1/n_2)}} \right\} = 1 - \beta.$$

The difference on the left side of the inequality in (7) is distributed under H_A as a central t-distribution. Therefore, the difference on the right side of the inequality in (7) can be set equal to a central t, analogous to (5), i.e.

$$(8)\quad t_{\nu,1-\beta} = t_{\nu,\alpha} - \frac{\bar{X}_1 - \bar{X}_2}{\sqrt{s_p^2\,(1/n_1 + 1/n_2)}}.$$

If the first sample has already been obtained, then n_1 and estimates of $\bar{X}_1$ and s_1^2 are available. Using s_1^2 as an estimate of,

$$(9)\quad t_{\nu,1-\beta} = t_{\nu,\alpha} - \frac{\bar{X}_1 - \bar{X}_2}{\sqrt{s_1^2\,(1/n_1 + 1/n_2)}},$$

where the degrees of freedom are appropriately reduced to (Baker 1935)

$$(10)\quad \nu = n_1 - 1$$

instead of

$$(11)\quad \nu = n_1 + n_2 - 2.$$

General discussions of the concepts of statistical power of a significance test and minimum detectable difference may be found in McCaughran (1977), Sokal and Rohlf (1969, section 7.8), and Zar (1975), although none of these references provides explicit development of the above types of equations.

In the present application the null and alternative hypotheses are most usefully defined in terms of a mean fractional reduction in year-class strength for 1978 and later years relative to the mean year-class strength before 1978. Thus, we define the mean of the second sample ($\bar{X}_2$) as a fraction ($1 - b$) of the mean of the first sample ($\bar{X}_1$), i.e.

$$(12)\quad \bar{X}_2 = (1 - b)\,\bar{X}_1,$$

where b is the fractional reduction in mean year-class strength for the period starting 1978, with possible values ranging from 0.0 (i.e. no reduction and $\bar{X}_2 = \bar{X}_1$) to 1.0 (i.e. the white perch population is eliminated and $\bar{X}_2 = 0.0$). Note that because of the one-tailed form of the alternative hypothesis (2), we are not considering cases with b less than zero (i.e. an increase in year-class strength for the period starting 1978 such that $\bar{X}_2 > \bar{X}_1$).

The difference between the two sample means in (9) may now be expressed as

$$(13)\quad \bar{X}_1 - \bar{X}_2 = \bar{X}_1 - (1 - b)\bar{X}_1 = b\,\bar{X}_1),$$

and (9) becomes

$$(14)\quad t_{\nu,1-\beta} = t_{\nu,\alpha} - b\,\bar{X}_1/\left(s_1\sqrt{1/n_1 + 1/n_2}\right) = t_{\nu,\alpha} - b/\left(\mathrm{CV}\sqrt{1/n_1 + 1/n_2}\right),$$

where CV ($= s_1/\bar{X}_1$) is the coefficient of variation for the sample of indices of year-class strength before 1978.

Addressing the first question posed in the introduction requires that (14) be solved for b, the fractional reduction in year-class strength for the period starting 1978. Since a central t-distribution is symmetrical about 0.0,

$$t_{\nu,1-\beta} = -\,t_{\nu,\beta},$$

and (14) can be arranged as

$$(15)\quad b = (t_{\nu,\alpha} + t_{\nu,\beta})\,\mathrm{CV}\sqrt{1/n_1 + 1/n_2}.$$

Then, for given values of α, β, n_1, and CV, one can solve (15) for a range of n_2 values to explore how b, the fractional reduction in the year-class strength of young-of-the-year white perch in the Hudson River, varies as a function of the number of years (starting with 1978) for which indices of year-class strength are available. Note in (15) that as n_2 becomes very large, the fractional reduction approaches a lower bound, B, given by

$$(16)\quad B = (t_{\nu,\alpha} + t_{\nu,\beta})\,\mathrm{CV}\sqrt{1/n_1}.$$

Addressing the second question posed in the introduction requires that (14) be solved for n_2, the number of years (starting with 1978) for which indices of year-class strength are available:

$$(17)\quad n_2 = \frac{(\mathrm{CV})^2\,n_1\,(t_{\nu,\alpha} + t_{\nu,\beta})^2}{b^2\,n_1 - (t_{\nu,\alpha} + t_{\nu,\beta})^2\,(\mathrm{CV})^2}.$$

Then, for given values of α, β, n_1, and CV, one can solve (17) for a range of b values to explore how the number of years of additional data (starting in 1978) varies as a function of the minimum fractional reduction in year-class strength that one wishes to be able to detect.

Results

Application of (15) and (17) requires that the coefficient of variation (CV) be specified. To make this analysis of statis-

tical power as relevant as possible to the two questions posed in the introduction, coefficients of variation associated with beach-seine indices and impingement-rate indices of year-class strength for the young-of-the-year white perch population in the Hudson River were examined (Van Winkle et al. 1980, appendix D). Based on this analysis we selected 50 and 100% for use as CV in (15) and (17).

Application of (15) and (17) also requires specification of values for α and β, the Type I and Type II errors, respectively, and of n_1, the number of years of impingement-rate data available for the period before 1978. We selected only one value of α ($\alpha = 0.05$), which means that we are accepting a 5% risk of falsely rejecting the null hypothesis of no reduction in year-class strength in favor of the set of one-tailed alternative hypotheses that there is a reduction. For each of the two values of the coefficient of variation, we selected a range of values of β to illustrate the importance of the concept of the power of a statistical test. The value of n_1 is 5, corresponding to the period 1973 through 1977.

The answer to the first question posed in the introduction is illustrated in Fig. 1. For example (Fig. 1b), if the coefficient of variation is assumed to be 50% and if impingement data are collected for the next 10 years (1978–87), then there is only a 10% chance ($= 1 - \beta$) that a reduction in mean year-class abundance of 16% would be detected. The smallest fractional reduction that can be detected with a probability of 50% or higher given 10 additional years of data is 0.58, and the smallest that can be detected with a probability of 75% or higher is 0.79. For a coefficient of variation of 100%, the situation is far worse (Fig. 1a). In this case there is only a 25% chance that a fractional reduction of 0.76 would be detected with 10 more years of data, and there is essentially no level of impact short of extinction that could be detected with a probability of 50% or higher.

The answer to the second question posed in the introduction is illustrated in Fig. 2. For example (Fig. 2b), if the coefficient of variation is 50% and if it is necessary, perhaps as directed by a regulatory agency, to be able to detect a 50% reduction in the mean size of the young-of-the-year white perch population in the Hudson River, 3 years ($1 - \beta = 0.25$) or 47 years ($1 - \beta = 0.50$) of additional impingement data (starting in 1978) would be required. Again, this result depends on the risk we are willing to take of concluding that there has been no statistically significant reduction in mean year-class strength when in fact there has been.

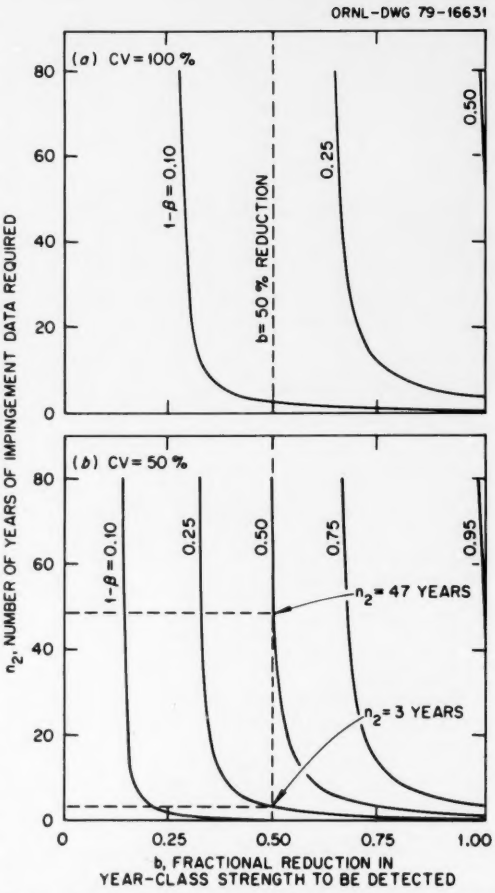

FIG. 1. Fractional reduction in mean year-class strength of young-of-the-year white perch in the Hudson River as a function of the number of additional years for which impingement data are available (starting in 1978). Curves are drawn for $\alpha = 0.05$ over a range of powers ($1 - \beta$), for $n_1 = 5$ years of pre-1978 data and for two values of the coefficient of variation (CV): (A) CV = 100% and (B) CV = 50%. Values of b on the figure are the minimum fractional reductions that could be detected, for the specified statistical powers, given 10 years of additional data.

Discussion

Our results are not encouraging. They indicate that the variability in the existing baseline time series of impingement rates is so great that: (a) 10 additional years of indices of year-class strength are not likely to provide a very powerful data set for detecting even substantial, actual reductions in mean year-class strength; and (b) a number of years greater than the expected lifetime of the power plants involved (e.g. 40 years) of additional data would be required to detect an actual 50% reduction in the mean index of year-class strength, even if one is willing to accept a Type II error as large as 50%.

In some cases the baseline impingement rates may not conform to the assumption of normality upon which the t-statistic (3) is based. For example, some fish species exhibit dominant year-class phenomena, so that a test for normality would probably result in rejection of the null hypothesis of normality (due to skewness to the right). In these cases, a logarithmic transformation may be used on the baseline impingement rates to normalize approximately the distribution. This transformation will tend to reduce the coefficient of variation. However, the parameter b no longer represents the fractional reduction in the mean of the transformed estimates of year-class strength.

A second assumption implicit in our use of the t-statistic is that the indices of year-class strength used to calculate $\bar{X}_1$ (3)

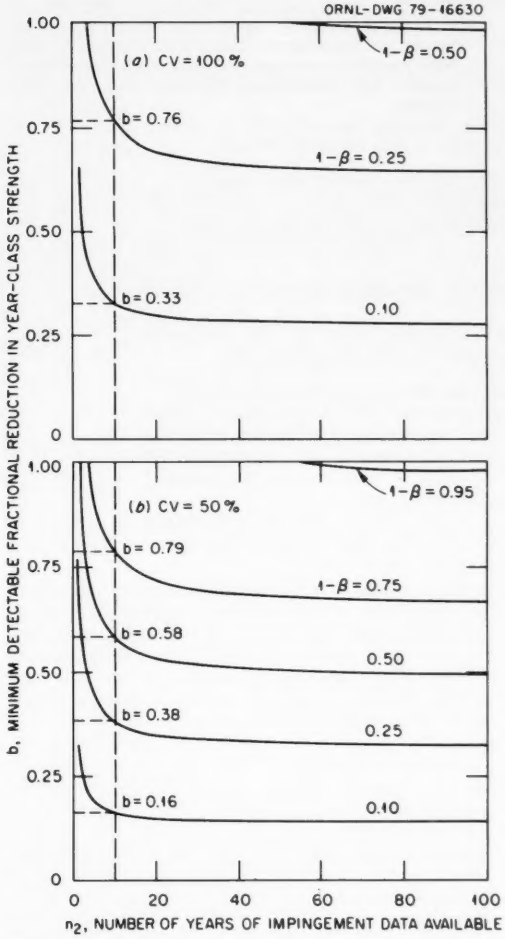

FIG. 2. Number of years of additional impingement data (starting in 1978) required to detect a specified fractional reduction in mean year-class strength of young-of-the-year white perch in the Hudson River. Curves are drawn for $\alpha = 0.05$ over a range of powers $(1 - \beta)$, for $n_1 = 5$ years of pre-1978 data and for two values of the coefficient of variation (CV): (A) CV = 100% and (B) CV = 50%. Values of n_2 on the figure are the number of additional years of data required, for the specified statistical powers, to detect a 50% reduction in mean year-class strength.

are independent. For some fish populations, such as the American shad (*Alosa sapidissima*) population in the Connecticut River where it has been shown that year-class strength is a function of the size of the spawning stock (Leggett 1977), this assumption is not strictly valid. However, for the Hudson River white perch population it appears that year-class strength is not that dependent on stock size, and our assumption of independence seems valid in this particular case.

The power of our statistical test can be increased (with the desired lowering of the minimum fractional reduction in mean year-class strength that could be detected and with the desired decrease in the number of additional years of impingement data required to detect a specified fractional reduction) if one accepts a larger probability of Type I error. That is, one can declare, from the standpoint of environmental protection and economic preservation of the fishery, that the balance between Type I and Type II errors ought to swing toward lowering the latter at some expense of increasing the former. The use of a 5% significance level is conventional, but not sacrosanct.

The methodology presented in this paper is applicable whenever a time series of indices of year-class strength is available. Because fluctuations in year-class strength of the Hudson River white perch population are not unusually great compared to those for other fish populations, it seems likely that similar results would be obtained for other species, even if the historical time series already available is appreciably longer. Thus, our analysis of the minimum detectable reduction in year-class strength of the Hudson River white perch population highlights a common prediction problem which is already well recognized but seldom quantified in environmental impact analyses. Our methodology offers a generic tool for establishing bounds on minimum detectable reductions in fish stocks (or other populations) and on the number of additional years of data required to be able to detect a specified reduction.

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On Some Cossuridae and Maldanidae (Polychaeta) from Washington and British Columbia[1]

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BANSE, K. 1981. On some Cossuridae and Maldanidae (Polychaeta) from Washington and British Columbia. Can. J. Fish. Aquat. Sci. 38: 633–637.

Cossura soyeri Laubier and *Clymenella torquata* (Leidy) are newly recorded for the Pacific Ocean. *Praxillella praetermissa* (Malmgren) is new to the northeast Pacific. Another species of *Cossura* (unidentifiable) and *Maldanella harai* (Izuka) are added to the fauna of Washington and British Columbia.

Key words: Cossuridae, Maldanidae, new records, Northeast Pacific, Polychaetes

BANSE, K. 1981. On some Cossuridae and Maldanidae (Polychaeta) from Washington and British Columbia. Can. J. Fish. Aquat. Sci. 38: 633–637.

Il s'agit d'une mention nouvelle dans l'océan Pacifique de *Cossura soyeri* Laubier et de *Clymenella torquata* (Leidy). *Praxillella praetermissa* (Malmgren) est signalé pour la première fois dans le Pacifique nord-est. Une autre espèce de *Cossura* (non identifiable) et *Maldanella harai* (Izuka) sont des additions à la faune de l'État de Washington et de la Colombie-Britannique.

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DURING the now completed study of new collections and the checking of earlier records of polychaetes from Washington and British Columbia (Hobson and Banse 1981), members of the Cossuridae and Maldanidae were found, which require some comment. A species of the former family was first reported from the region by Berkeley and Berkeley (1956). An addition to the description of probably the same species was made by Banse (1963). Herein, the species as found by Berkeley and Berkeley (1956) is partially redescribed and reassigned, and new material is recorded. The earlier research on Maldanidae of the region was summarized by Berkeley and Berkeley (1952) and Berkeley (1968). Comments on some species and new records were provided by Banse and Hobson (1968), Banse et al. (1968), and McDaniel and Banse (1979). The present paper adds three maldanid species to the northeast Pacific fauna and corrects some of the records of *Maldanella robusta* Moore from British Columbia.

COSSURIDAE

Cossura soyeri Laubier

Cossura soyeri Laubier, 1964: 833 — Gardiner and Wilson 1979: 169.

Cossura longocirrata [not Webster and Benedict, 1887] — Berkeley and Berkeley 1956: 544 — Banse 1963: 204 — Nichols 1968: 59.

MATERIAL: Washington: Orcas I., East Sound, about 27 m, mud (National Museum of Natural History, Smithsonian Institution, No. USNM 40305, 2 specimens [see Berkeley and Berkeley 1956]) — Port Madison, Stas. F, J, K of Nichols (1968), approximately 47°44′N, 122°32′W, muddy sand, 13–32 m, Oct. 21–22, 1965. Coll. by F. H. Nichols (Friday Harbor Laboratories, University of Washington, No. FHL 1354, several specimens) — Orcas I.: Massacre Bay, about 48°38.0′N, 122°59′W, 14 m, mud, July 1967 (USNM 42014, 25 specimens); Harney Pass, about 48°35.5′N, 122°55′W, 27 m, mud, July 1967 (FHL, about 10 specimens); West Sound, about 48°36′N, 122°57′N, 40 m, mud, July 1967 (last three collections by H. L. Sanders, together about 75 specimens; all stations new records).

DESCRIPTION: The prostomium is conical in dorsal view. It is followed by two achetous segments which together are slightly longer than the first, uniramous setiger. The tentacle inserts at the posterior border of the next segment which is biramous (setiger 2). Approximately the first 30 setigers are crowded and followed by swollen (and in some animals beaded) segments with sexual products. The anal cirri are unbranched and arranged as described by Berkeley and Berkeley (1956; see also Gardiner and Wilson 1979). No posterior end was available to Laubier (1964) for the original description.

Both parapodial rami, from setiger 2 onwards, possess an anterior fan of short, tapered, capillary setae with fine hairs at the edge; the setae are of the form as depicted by Kitamori (1960, fig. 1F) for *C. coasta* Kitamori, or are slightly more tapered. The setae of the posterior fan are longer, having a proximal half of the same form and dimension as the anterior ones but a long drawn-out distal section that is almost free of

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hairs. Setae at about segment 40 are limbate and gradually drawn into very fine tips, with some within one ramus being maximally 5 μm wide and about 0.1 mm long, and others having the same width but twice that length.

Animals collected in October (F. H. Nichols coll.) had segments from about setiger 17 packed with polygonal to oval eggs with dimensions of about 100 μm × 150 μm.

REMARKS: The identification with Laubier's species is based on the specimens collected in 1967. A reexamination of the material of Berkeley and Berkeley (1956) showed that two achetous segments [not one] are followed by a uniramous setiger. The next segment has indistinctly biramous parapodia and carries the tentacle. My material described in 1963, also from West Sound, Orcas I., has been lost, but two achetous segments were present and the tentacle inserted at the posterior border of setiger 2. There is thus good reason to believe that all records are of the same species.

New record. Previously known from the Mediterranean and the warm-temperate North American east coast.

Cossura sp.

MATERIAL: British Columbia: Chatham Sd off Ridley I., 54°14′N, 130°20′W, mud, 18 m, July 10, 1974. Coll. by Envir. Prot. Serv. Can., Sta. CS-3 (British Columbia Provincial Museum, No. BCPM 974-628-1, 1 specimen).

Washington: Orcas I., West Sound (one specimen from material of H. L. Sanders [see under *C. soyeri*]).

DESCRIPTION: The well-preserved anterior end from British Columbia possesses 30 setigers and is about 3.5 mm long. The conical prostomium is followed by two achetous rings which together are slightly shorter than the first, uniramous setiger and are not as distinct as in *C. soyeri*. The tentacle inserts at the posterior border of setiger 3; this border bulges middorsally into setiger 4. All setigers, from 2 onwards, are biramous and have the same setae as described above for the anterior body portion of *C. soyeri*.

One anterior fragment of the collection by Sanders, now apparently lost, seems to have been the same species: with about 20 setigers, it was 2.2 mm long and 0.4 mm wide and thus twice as large as the (mature) specimens of *C. soyeri*. The only apparent difference between this species and *C. soyeri* was the insertion of the tentacle on setiger 3 rather than setiger 2.

REMARKS: The fragments cannot be specifically identified because of the missing posterior end (cf. key in Fauchald 1972), but they do constitute the addition of a species to the fauna of British Columbia and Washington.

MALDANIDAE

Clymenella torquata (Leidy)

Clymene torquatus Leidy, 1855: 146 [not consulted].
Axiothea torquata — Lewis 1897: 111.
Clymenella torquata — Hartman 1945: 40 — Newell 1949: 147.

MATERIAL: British Columbia: Boundary Bay, northern shore, about 49°N,123°W, many intertidal stations among eelgrass, approximately between +1 and 2 m above Canadian datum level. February 1980. Coll. by D. Gordon (BCPM 980-410-1, 2 specimens; Environment Canada, Fish. and Ocean, West Vancouver Lab., 4 specimens).

DESCRIPTION: Some of the worms, up to about 50 mm long, carry eggs. They agree with the detailed description by Newell (1949) except that the pygidial cirri are triangular and shorter than in the British material; the cirri are very much like those depicted from Beaufort, N.C., by Lewis (1897; pl. 1, fig. 7) and those of the local *Isocirrus longiceps* (Moore). The number of cirri varies from 19 to 24 (largest individual). The first three setigers bear between five or six and more than 10 slightly modified uncini. While uncini in the middle region of the body of one specimen checked had four secondary teeth (five in the British material of Newell 1949), the posterior (setiger 16) uncini had only three and further lacked the subapical hairs.

REMARKS: Three other North Pacific species previously had been assigned to *Clymenella* Verrill: *C. tentaculata* Moore, 1906 from the Gulf of Alaska, and *C. complanata* Hartman, 1969 and *C. californica* Blake and Kudenov, 1974 from California. None of these is similar to the present species. *Clymenella tentaculata* is based on one anterior and one posterior piece which may be part of the same individual. It is particularly distinguished by a fingerlike palpode that is reminiscent of that of *Praxillella gracilis* (Sars). Further, the three to five uncini of the first three parapodial tori are modified such that the rostrum forms only a slight angle with the shaft of the uncinus. Also there is no collar. Considering the uncertainty about the posterior end, it is thus possible that this form is not a species of *Clymenella*. Certainly, however, the two Californian species should not be included in the genus for which *C. torquata* is the type species because they possess neuropodial single spines in the anterior three setigers. Moreover, the cephalic plate of *C. complanata* is very different from *Clymenella* s. str. where it is similar to that of *Euclymene*. No suggestion can be made, however, for a more convincing assignment of the two species because of the uncertainty surrounding the generic diagnoses of *Clymenella* and *Axiothella* (see e.g. Arwidsson 1907: 209, and Clark and Dawson 1963, under *C. cincta*).

Clymenella torquata is new to the Pacific Ocean. Previously, it was known from New England to Florida as well as from England where it is suspected to be a recent import accompanying oysters (Newell 1949). The apparently disjunct geographic distribution of the species in North America might likewise be explained by human intervention because between 1906 and about 1936, oysters from the North American east coast were planted in Boundary Bay (Quayle 1964) where *C. torquata* now occurs extensively. On the other hand, the intertidal zone of British Columbia and Washington has recently yielded several new records of macroscopic, common polychaetes of which at least one (*Hobsonia florida*, cf. Banse 1979) has certainly occurred there for decades so that possibly, *C. torquata* also lives elsewhere on the North American west coast.

The occurrence of the species in Boundary Bay corresponded fairly well with the eelgrass zone. The mean abundance (from 40-cm-diameter cores, sieved through a 0.5-mm screen) was 416/m^2 (SD, ±375; range, 16 to 1680; 20 stations).

Maldanella harai (Izuka)

Clymene harai Izuka, 1902: 111 — Arwidsson 1907: 127.
Axiothea campanulata Moore, 1903: 485 — 1906: 239 [under *Maldanella robusta*] — Arwidsson 1907: 128.
Maldanella harai — Moore 1906: 239 [under *Maldanella robusta*] — Hartman 1959: 461 — Imajima and Hartman 1964: 319 — Hartman 1971: 1423 — Pereyra and Alton 1972: 449.
?*Maldanella harai* — Fauvel 1927: 186.
Maldanella robusta [not Moore, 1906] — Berkeley and Berkeley 1952: 51.

MATERIAL: Japan: Suruga Bay, off Honshu (U.S.S. Albatross Sta. 3739), 100–117 m (55–65 fms), May 17, 1900. Holotype of *Axiothea campanulata* Moore, 1903 (USNM 16145).

British Columbia: Queen Charlotte I. Coll. by E. and C. Berkeley, ident. [as *M. robusta*] (USNM 40755, 1 specimen) — Trevor Channel, 48°52.0′N, 125°09.5′W, sand–mud–shell, 27–51 m, April 14, 1975. Coll. by K. D. Hobson, ident. [as *M. robusta*] (BCPM 975-167-3, 1 specimen).

Washington: Strait of Juan de Fuca, 48°22.4′N, 124°26.3′W, gravel with mud, 140 m, June 12, 1975. Coll. by K. D. Hobson, ident. [as *M. robusta*] (private coll., K. B., 1 specimen).

DESCRIPTION: The specimens from British Columbia and Washington all have two posterior achetous segments (see fig. 11*s* in Hobson and Banse 1981), and nephridial papillae on setigers 6–8.

REMARKS: Moore (1906) placed *Axiothea campanulata* Moore, 1903 in synonymy with *M. harai*. The holotype of *A. campanulata* has nephridial papillae on setigers 6–8 as does the holotype of *M. robusta* Moore, 1906 (USNM 5526). The holotype of *M. robusta* lacks the posterior end so that the most obvious difference between *M. harai* and *M. robusta*, the number of achetous posterior segments, cannot be ascertained; M. H. Pettibone of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (unpublished; according to label dated 1951 in USNM 5526) believed *M. robusta* to be a synonym of *M. harai*. However, the rim of the cephalic plate of *M. harai* is smooth while that of *M. robusta* is crenulated. The description of *M. robusta* by Berkeley and Berkeley (1952), presumably based on the specimen from the Queen Charlotte Is., refers to *M. harai* because text and fig. 104 show two achetous posterior segments.

Maldanella harai, originally described from Japan (Izuka 1902) and now reported from British Columbia and Washington had previously been recorded from Oregon (Pereyra and Alton 1972 [M. H. Pettibone ident.]) and from the deep sea (Fauvel 1927; Hartman 1971). Fauvel's record, however, may represent a different species as both his text and fig. 64*n* indicate that the nuchal organs are not V-shaped as in *M. harai*; also, the posterior end of the specimen studied by Fauvel (fig, 64*l*), does not show the bell-shaped, typical pygidium of the animals available to me.

Praxillella praetermissa (Malmgren)
Fig. 1

Praxilla praetermissa Malmgren, 1865: 191.
Praxillella praetermissa — Arwidsson 1907: 192 — Pettibone 1954: 303 — Hartmann-Schröder 1971: 424 [not consulted].

MATERIAL: Washington: Orcas I., West Sound, about 48°36′N, 122°57′W, 40 m, mud, July 1967. Coll. by H. L. Sanders (K. B., private collection, several specimens).

DESCRIPTION: The sample contains two complete specimens and several longer but broken animals. The two complete specimens measure about 10 and 16 mm and possess 19 setigers (one has notosetae on one side in a 20th setiger) and four posterior achetous segments. The anterior end is provided with a marked cephalic rim without lateral incision. Arwidsson (1907, pl. 4, fig. 137*a*) reported the species to have a cephalic rim with a lateral incision. The palpode is obtuse. The nuchal organs extend over almost two-thirds of the cephalic plate. The prostomium and setiger 3 bear diffusely distributed epidermal glands which may be distinguished clearly only after staining with methyl green in alcohol. The other anterior setigers are glandularized between

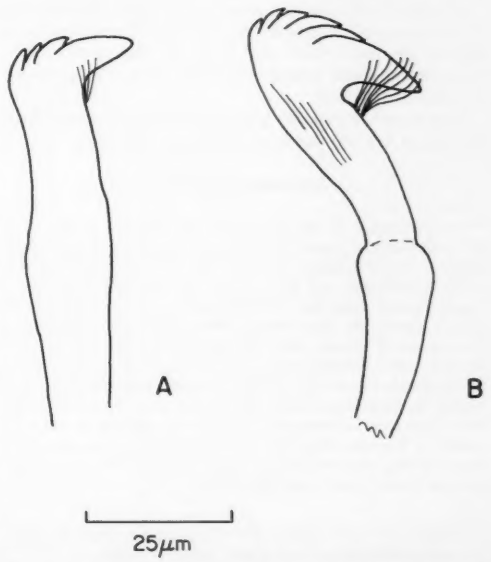

FIG. 1. *Praxillella praetermissa*: A, neuroseta from setiger 1; B, neuroseta from setiger 8.

their anterior borders and the level of the parapodia, weakly so in setiger 2 but in a bandlike pattern from setigers 4 to 8 (in one case, to 9). In the subsequent setigers, scattered stained cells are present around the parapodia.

The first two of the four posterior, achetous segments bear parapodia while the two last segments are mere rings. Between the last segment and the pygidium is another ring of the same diameter but with a different epidermal structure. In all specimens, the last two segments and the last mentioned ring are very short, ~one-eighth as long as they are wide. The anus, provided with a conspicuous valve, is not visible in side view, being withdrawn into a funnel in all specimens. The number of pygidial cirri varies from about a dozen in the smallest, to about two dozen in the largest animals.

A neuroseta representative for those of the first three setigers is depicted in Fig. 1A; three to four are present per torus. Posteriorly, more than 12 neurosetae as in Fig. 1B are found in a torus. Arwidsson (1907) stresses, as typical for *P. praetermissa*, that the subapical hairs cover the beak of the hooks on both sides, as is the case here. The notosetae are smooth (checked on setiger 8).

REMARKS: The presence of a withdrawn anal cone differs from the original description of *Praxillella praetermissa* and might suggest placement of the animals in *Euclymene* Verrill. However, my specimens otherwise greatly resemble *P. praetermissa* for which Arwidsson (1907, pl. 4, fig. 142; see also in footnote, p. 175 and p. 176, bottom) noted the tendency to form a pygidial funnel. The animals clearly do not belong to one of the other temperate North Pacific species of *Praxillella* (cf. Berkeley and Berkeley 1952; Ushakov 1955; Imajima and Hartman 1964; Hartman 1969).

A band of epidermal glands occurs on setiger 9 in only one of the specimens. If the identification with *P. praetermissa* is correct, the band would cast doubt on the validity of *P. praetermissa minor* Arwidsson (1907) which is based on the presence of this band.

New record. Previously known in the Pacific Ocean from the Bering Sea and the Seas of Okhotsk and Japan.

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Environmental Control of Phytoplankton Patchiness

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THERRIAULT, J.-C., AND T. PLATT. 1981. Environmental control of phytoplankton patchiness. Can. J. Fish. Aquat. Sci. 38: 638–641.

The relative importance of the various biological, chemical, and physical factors for the control of the phytoplankton patchiness in the environment has been studied for the near-surface waters of a small coastal embayment. It was found that during periods of low turbulent mixing (wind speed ≤5 m/s), the phytoplankton patchiness was induced by local differences (taxonomic or physiological) in its production efficiency which was linked to the dynamic fluctuation in the physicochemical characteristics of the medium. For periods of high winds (≥5 m/s) it is indicated that the physical turbulent transport processes were responsible for damping out the spatial variations in the phytoplankton distribution.

Key words: phytoplankton biomass, P/B ratio, spatial distribution, turbulence, wind stress

THERRIAULT, J.-C., AND T. PLATT. 1981. Environmental control of phytoplankton patchiness. Can. J. Fish. Aquat. Sci. 38: 638–641.

L'importance relative des facteurs physiques, chimiques et biologiques sur le contrôle et la formation de taches de phytoplancton dans l'environnement a été étudiée pour les eaux de surface d'une petite baie côtière. Nous avons trouvé que pour les périodes de mélange turbulent faible (vitesse du vent ≤5 m/s), les taches de phytoplancton se formaient à partir de différences locales (taxonomiques ou physiologiques) dans la capacité de production qui, elle, est liée aux fluctuations dynamiques des caractéristiques physico-chimiques du milieu. Pour les périodes de fort mélange (≥5 m/s), on a trouvé que les processus de transport physique turbulent tendent à éliminer les différences spatiales dans la distribution du phypoplancton.

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IT is becoming accepted (Steele 1978; Platt et al. 1981) that the variances are equally as important, or more important, than the mean values of state variables in controlling ecosystem dynamics. Spatial variance of biomass or resources is called "patchiness." In the pelagic ecosystem of the sea, the physical determinant of patchiness, the coefficient of turbulent diffusion, is quantifiable (Steele 1974), but the processes by which patchiness is mediated are not fully understood (Steele 1978). Here we report evidence for direct environmental control of the patchiness of phytoplankton turnover in a near-shore ecosystem.

Materials and Methods

Collection of the data has already been described (Therriault and Platt 1978; Therriault et al. 1978). Briefly, phytoplankton turnover (primary production per unit chlorophyll biomass) was measured on 30 occasions throughout 1 year at a fixed depth (5 m) on six stations distributed at random in an area of about 12 km^2 in St. Margaret's Bay, Nova Scotia. At each station, the measurements were replicated sufficiently well that it was possible to estimate the component of variance due to real differences between stations. Further replicated samples were taken and analyzed for inorganic nutrients, pheopigments, particulate carbon, and nitrogen. Wind stress was measured as the vector average of readings from two anemometers positioned on opposite sides of the bay.

Results and Discussion

Wind stress was highly variable throughout the year, but was in general lower (≤5 m/s) during summer (Fig. 1a). For each sampling day, the between-station variance (patchiness) in phytoplankton turnover (P/B) was computed (Fig. 1b). No consistent relationship could be found throughout the year between the spatial variance in P/B and the spatial variances

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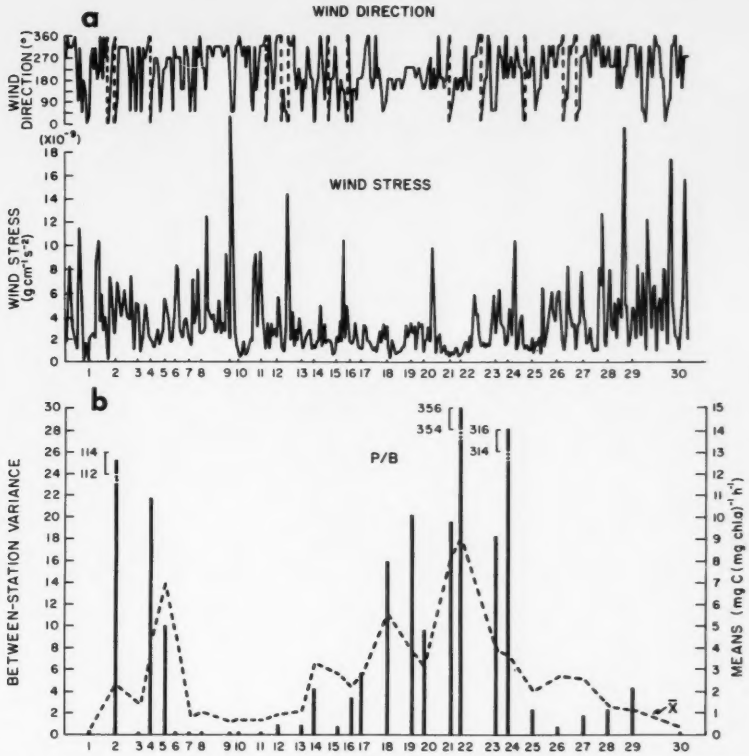

FIG. 1. Plot of (a) the daily means of the wind stress and direction (*upper part*) as function of time for the period of a whole year in 1975 and (b) of the estimate of the between-station variance (taken from Therriault et al. 1978) and the mean value of the P/B ratio for each sampling day (1−30).

of the other measurements (Therriault and Platt 1978). We determined by stepwise linear regression how much of the variance in Var (P/B) could be explained by wind stress (averaged over 72 h before measurement) and the variances of dissolved ammonia, nitrate, silicate, pheopigments, and the carbon to nitrogen (C/N) ratio of the phytoplankton.

When data from all 30 cruises were pooled (Table 1a), wind stress and the variances in C/N and in ammonia accounted for roughly equal proportions of the variance in Var (P/B), that is, 13, 14, and 13%, respectively. If the data were analyzed separately for measurements preceded by winds greater or less than 5 m/s, wind stress was the only significant independent variable for winds $\geq$5 m/s (Table 1c), but had no significant effect for winds $\leq$5 m/s, when 88% of the variance in Var (P/B) could be accounted for by biological variables (Table 1b).

We interpret these results as follows. The threshold wind speed of 5 m/s is that at which wind stress begins to exert a measurable mixing effect on the surface layer in near-shore waters (Kullenburg 1971, 1972, 1974, 1976). Furthermore, we have shown directly (Therriault et al. 1978) a strong, positive dependence of horizontal current variance (averaged over current metres moored at two stations during 8 wk of the study) on wind stress. The data taken on days preceded by winds in excess of 5 m/s, then, correspond to physical turbulent periods. In this case, the variance in phytoplankton turnover is dominated entirely by physical processes. Wind stress accounts for 41% of the variance in a linear model, or 80% in a nonlinear model (Table 1d) as suggested by the results in Therriault et al. (1978). Moreover, an increase in wind stress causes a decrease in the spatial variance in P/B: that is, turbulence tends to erode patchiness.

On the other hand, for winds $\leq$5 m/s (physically quiet periods) the spatial variance of P/B is explained by biological variables only. Changes in the C/N ratio are taken to reflect changes in the chemical composition of the phytoplankton, through either its physiological state or, more likely, its community structure (Antia et al. 1963; Strickland et al. 1969; Caperon and Meyer 1972). Increasing spatial variance in chemical composition (C/N ratio) leads to increased patchiness in P/B and is probably indicative of taxonomic differences. However, when spatial differences are observed in Var (P/B), but not in the C/N ratio or in the other variables, as for example at the onset of the spring bloom (sampling days 2, 4,

TABLE 1. Summary of the stepwise linear regression analyses using data for (a) all sampling days (30 cruises); (b) the sampling days characterized by a wind velocity (previous 72 h) ≤5 m/s; (c) and (d) the sampling days with previous wind velocity ≥5 m/s. The quantity R is the cumulative multiple correlation coefficient. ΔR^2 is the increase in the amount of the variance in the independent variable which is explained by including a particular variable in the regression. The dependent variable in each case is the spatial variance of P/B.

Independent variables	Regress. coeff.	SE of regress. coeff.	Cumulative R	ΔR^2
		(*a*)		
Var. C/N ratio	53.675	10.750	0.3799	0.1443
Wind stress	−0.077	0.067	0.5219	0.1280
Var. pheopigment	9.588	2.365	0.5844	0.0692
Var. ammonia	−33.797	10.336	0.6851	0.1278
Var. nitrate	−7.997	3.200	0.7420	0.0812
Var. silicate	−11.370	4.765	0.7998	0.0892
Constant term	54.510			
		(*b*)		
Var. C/N ratio	67.886	11.669	0.6529	0.4263
Var. ammonia	−33.572	9.122	0.7110	0.0792
Var. pheopigment	12.819	2.343	0.8387	0.1979
Var silicate	−39.156	10.906	0.9225	0.1476
Var. nitrate	−5.361	4.551	0.9318	0.0172
Wind stress	−0.215	0.165	0.9411	0.0175
Constant term	36.699			
		(*c*)		
Wind stress	−0.039	0.016	0.6425	0.4128
Constant term	25.230			
		(*d*)		
Log of wind stress	−6.821	1.145	0.8930	0.7980
Constant term	18.579			

and 5), differences in the physiological state of the population alone can probably account for the observed patchiness in P/B. Amount of pheopigment in the particulate matter is taken to be an index of grazing by herbivorous zooplankton (Currie 1962; Shuman and Lorenzen 1975): the more nonuniform it is in space, the more variable the phytoplankton turnover. Note that for these quiet periods, wind stress adds no significant information useful in explaining the variance of phytoplankton turnover.

We thus have evidence for two distinct regimes. We believe that this result is not location-specific: it corresponds well with the theoretical and observational data of Kullenberg (1976). If winds are strong enough to surpass the threshold for surface layer mixing, they dominate all other potential sources of variance in P/B. On the other hand, in periods of wind stress below this threshold, spatial variance in P/B can be ascribed to biological causes. These results are consistent with the notion that local and short-term evolution of the plankton structure proceeds according to the biological dynamics unless and until it is disturbed by physical processes (Platt and Denman 1980). On the more practical side, a similar demonstration of the effect of wind on the sampling variance of plankton (in this case plaice eggs) was given by Cushing (1955).

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Effect of Sedimentation on Infaunal Invertebrate Populations of Cobequid Bay, Bay of Fundy

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TURK, T. R., AND M. J. RISK. 1981. Effect of sedimentation on infaunal invertebrate populations of Cobequid Bay, Bay of Fundy. Can. J. Fish. Aquat. Sci. 38: 642–648.

Construction of a tidal dam in the upper reaches of the Bay of Fundy is expected to result in deposition of sediment. We investigated the effect of sediment deposition on populations of three major benthic species of the upper reaches: *Corophium volutator, Macoma balthica,* and *Mya arenaria*. In fences and boxes that induced deposition on intertidal mudflats, accumulation of 1.0–3.5 cm of sediment at rates of 1.9–10.2 cm/mo caused *Corophium* density to decrease sharply, usually by an order of magnitude. *Macoma* density was generally unaffected. In fishing weirs, mud that accumulated at 1.5 cm/mo to a mean depth of 5.2 cm supported normal *Corophium* densities. The effect of sedimentation on *Mya* depends strongly on grain size: LD50 was 24 cm for coarse sand, 6 cm for fine sand, and 3 cm for mud. *Mya* is able to burrow upward in accumulating coarse sand. Even moderate rates and depths of sediment deposition, particularly of fine sediment, could have a major adverse effect on existing *Corophium* and *Mya* populations.

Key words: Bay of Fundy, tidal power, sedimentation, grain size, water content, *Corophium volutator, Macoma balthica, Mya arenaria*

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On s'attend que la construction d'un barrage de régulation des marées à la partie supérieure de la baie de Fundy causera une déposition de sédiment. Nous avons examiné l'effet d'une telle déposition sur les populations de trois principales espèces benthiques de ce secteur de la baie: *Corophium volutator*, *Macoma balthica* et *Mya arenaria*. Sur des claies et dans des boîtes provoquant la déposition sur des vasières infratidale, l'accumulation de 1,0–3,5 cm de sédiment à des taux de 1,9–10,2 cm/mois cause une abrupte diminution de densité de *Corophium*, ordinairement d'un ordre de grandeur. La densité de *Macoma* n'est généralement pas influencée. Dans des parcs de pêche, la vase qui s'accumule au taux de 1,5 cm/mois jusqu'à une profondeur moyenne de 5,2 cm supporte des densités normales de *Corophium*. La taille des particules influence fortement l'effet de la sédimentation sur *Mya*: la DL50 est de 24 cm pour le gros sable, 6 cm pour le sable fin et 3 cm pour la vase. Dans le gros sable qui s'accumule, *Mya* peut se frayer un chemin vers le haut. Une déposition de sédiment, surtout de fin sédiment, même à des taux et à des profondeurs modérés, pourrait nuire aux populations existantes de *Corophium* et de *Mya*.

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CONSIDERATION of the development of tidal power in the upper reaches of the Bay of Fundy has stimulated interest in potential environmental effects (Daborn 1977; Gordon and Longhurst 1979; Risk and Buckley 1979; Yeo and Risk 1979a; Turk et al. 1980). One of the major expected effects of a tidal dam is sediment deposition in both subtidal and intertidal areas of the upper reaches (Amos 1977; Greenberg 1979).

Such sedimentation will affect benthic populations. We were particularly interested in the effect of sediment accumulation on the infauna of Fundy intertidal flats. We used two basic approaches: (1) investigating organism densities in the mud that collected behind commercial fishing weirs (V-shaped structures about 100 m on each side, built of poles and brush and designed to catch fish on the falling tide), and (2) inducing sediment deposition by building fence- and box-shaped structures on intertidal flats. Discussion is limited to three of the most abundant infaunal species of this region,

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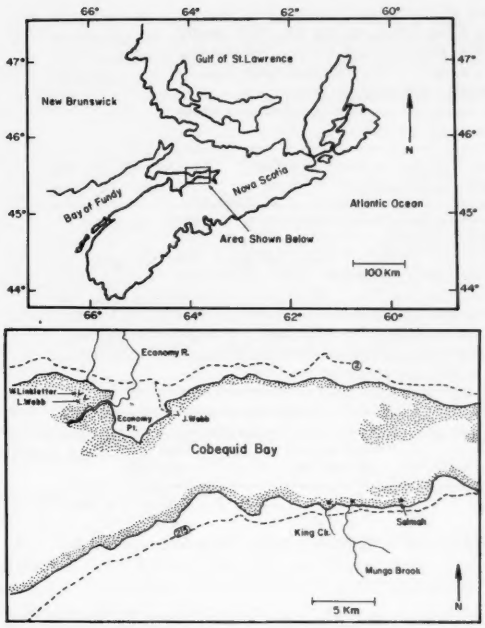

FIG. 1. Location of study areas. *Top:* the Maritime Provinces, showing the Bay of Fundy. *Bottom:* Cobequid Bay and study sites. Fish weirs were in the Economy Pt. region, fences at King Creek and Selmah, and boxes at Mungo Brook. Shaded area is intertidal zone.

the amphipod *Corophium volutator*, the small bivalve *Macoma balthica*, and the soft-shelled clam, *Mya arenaria*. For description of the intertidal benthic fauna of the upper reaches, see Risk et al. (1977), Thomas (1977), Yeo and Risk (1979a), and Risk and Yeo (1981).

Study Locations and General Methods

Study sites were in Cobequid Bay, the uppermost part of the southern arm of the Bay of Fundy (Fig. 1). Three fishing weirs were studied in the Economy Pt. region, on the northern shore of Cobequid Bay. Boxes were built at Mungo Brook, and fences at King Creek and Selmah, all on the southern shore.

At all sites, surface sediment cores were taken with a plastic tube 5 cm in diameter. Water content and grain size distribution were determined for sediment samples. Samples were dried to a constant weight at 110°C to determine water content. For grain-size analysis, dry sieving was used for material coarser than 62 μm (4.0ϕ) and standard pipette analysis for finer material, as outlined in Folk (1968) and Carver (1971). Prior to size analysis, samples were treated with H_2O_2 to remove organics. Calgon was used as the dispersant in pipette analysis.

Corophium volutator densities were determined by taking 8-cm-diameter sediment cores to a depth of 6 cm (*Corophium* rarely occur deeper). These samples were washed through 0.5-mm mesh screens and the retained *Corophium* counted. For *M. balthica*, a larger and generally less-abundant species, a 16-cm-diameter core was taken to a depth of 15 cm and washed through a 1.0-mm mesh. *Mya arenaria* were sampled by digging up $\frac{1}{4}$ or $\frac{1}{2}$ m^2 quadrats to 25 cm and sifting the sediment by hand.

In this paper, means (of density, grain size, water content), slopes, and elevations were compared using *t*-tests and standard parametric regression techniques (Zar 1974). In almost all cases, densities were calculated on the basis of large enough counts that violation of the assumptions of parametric tests was not serious. Data sets containing percentages between 30 and 70 were transformed to arcsine.

Fences

METHODS

Fences were constructed primarily of a solid piece of sheet metal, 8 m long and 1 m high, oriented perpendicular to the shoreline and supported by metal posts and by rock-filled cages (gabions) at each end.

The King Creek fence was built on a mudflat typical of the mid- to upper-intertidal zone of Cobequid Bay. This fence was used to test the effect of sedimentation on *C. volutator* and *M. balthica*; *M. arenaria* is rare in these mudflats. Construction was completed on June 20, 1979. Before fence construction and again after sediment accumulation, fauna and sediment samples were taken at random points in two $\frac{1}{2}$-m-wide strips, running the length (8 m) of each side of the fence and each displaced $\frac{1}{2}$-m from the fence. (The $\frac{1}{2}$ m nearest the fence on each side was kept as a walkway for building and repairing the fence.) Sampling dates and sample sizes are reported with the data in Tables 1 and 2. "Control" sediment and fauna samples were taken at the fence's tidal level in the mudflat, at sites nearby but far enough from the fence (~15 m) to be unaffected by it.

Changes in sediment depth near the fence were monitored by measuring the distance from the mud surface down to a total of 16 metal plates (~15 cm square) that were placed at regular intervals at a depth of 6–8 cm, in the same strips that were sampled for fauna and sediment. Six similar plates were placed around the fence, at a distance of ~15 m, to monitor changes in sediment depth in more distant areas.

The fence at Selmah was built in an intertidal gravel lag and coarse sand flat near Selmah Bar on the southern shore of Cobequid Bay (Fig. 1). This fence was used to test the effect of sedimentation on *M. arenaria* only. It was completed on July 6, 1979, and was sampled on August 12. Seventeen $\frac{1}{2}$-m^2 quadrats were excavated, the depth of accumulated sediment was measured to the nearest cm, and living and dead *Mya* (both in the accumulated sediment and in the underlying original sediment) were counted.

RESULTS

King Creek — Between June 20 and August 14, the two $\frac{1}{2}$-m strips near the King Creek fence accumulated a mean of 3.5 cm ($s = 1.10$, $n = 16$) of sediment. This represents a rate of 1.9 cm/mo. Accumulation away from the fence could not be distinguished from zero ($\bar{x} = -0.13$ cm, $s = 0.42$ cm,

TABLE 1. Mean density and standard deviation of *Corophium volutator* and *Macoma balthica* near, and ~15 m away from, the King Creek Fence, on June 16, 1979, shortly before fence construction, and on August 14, 1979, after 3.5 cm of sediment had accumulated near the fence. Each mean is based on a sample of 18. (*Increase since June 16 ($P < 0.005$), **decrease since June 16 ($P < 0.001$), otherwise, no change.)

	Mean densities (no./m^2)			
	Near fence		Away from fence	
	C. volutator	*M. balthica*	*C. volutator*	*M. balthica*
June 16	1666, s = 728	1523, s = 801	1695, s = 761	1415, s = 427
August 14	365**, s = 585	1472, s = 731	3545*, s = 2231	1332, s = 264

TABLE 2. Water content and mean grain size of top 2 cm of sediment near, and about 15 m away from, the King Creek fence, on June 16, 1979, shortly before fence construction, and on August 14, 1979, after 3.5 cm of sediment had accumulated near the fence. Means, standard deviations, and sample sizes are also shown. Large ϕ means finer sediment. (*$P < 0.05$ (compared to June 16), **$P < 0.001$ (compared to June 16), otherwise, no change.)

	Near fence		Away from fence	
	Water content (% wet wt)	Mean grain size (ϕ)	Water content (% wet wt)	Mean grain size (ϕ)
June 16	$\bar{x}$ = 36.2, s = 3.35, n = 6	$\bar{x}$ = 5.05, s = 0.387, n = 3	$\bar{x}$ = 33.6, s = 1.30, n = 4	$\bar{x}$ = 4.93, s = 0.391, n = 3
August 14	$\bar{x}$ = 24.4**, s = 1.30, n = 6	$\bar{x}$ = 3.95*, s = 0.332, n = 3	$\bar{x}$ = 28.3*, s = 3.26, n = 4	$\bar{x}$ = 5.16, s = 0.239, n = 3

$n = 6$).

During the same period, *Corophium* density decreased sharply near the fence (Table 1), but increased away from it (young-of-the-year *Corophium* become large enough to appear in these samples during this time). *Macoma* density did not change at either location.

Sediment water content and mean grain size near and away from the fence, from both sampling dates, are compared in Table 2. Water content decreased during the study both near and away from the fence. The decrease was greater near the fence, and water content was lower near the fence than away from it on August 14. This may be due to the coarser sediments that collected near the fence, since grain size and water content are usually inversely related.

Selmah — This fence collected up to 40 cm of coarse sand, apparently caused by shifting bedload rather than by deposition of suspended sediment. The proportion of the original *Mya* in a quadrat that was killed by sediment accumulation was directly and significantly ($P < 0.01$) related to the depth of the accumulation (Fig. 2, lowest regression line). The depth of sediment that resulted in the death of 50% of the *Mya* (LD50) was ~24 cm. In all quadrats except those with little accumulation, *Mya* survival was apparently enhanced by the ability of some individuals to burrow upward in the accumulated sand.

Boxes

METHODS

Boxes were placed on the intertidal mudflat at the Mungo Brook site, ~2 km east of King Creek (Fig. 1). These bottomless boxes were made of plywood and were 122 cm (4 fit) on a side and 61 cm (2 fit) high. They were pushed into the mud ~15 cm and were held in place by metal posts driven into bedrock at each corner. The difficulty of keeping the boxes in place resulted in short experiments and varying starting and ending dates. Only 4 of 12 boxes remained in place long enough to be useful.

In two of the boxes, sedimentation was augmented by adding mud collected from the slug of muddy water at the edge of the incoming and receding tide. This mud was strained through 0.5-mm mesh to remove macrofauna before it was added as a slurry when the boxes were partially flooded. Changes in sediment depth were determined by measuring the distance from the sediment surface to the tops of the boxes. On the beginning and ending dates, four *Corophium* and *Macoma* samples were taken from each box. On the end

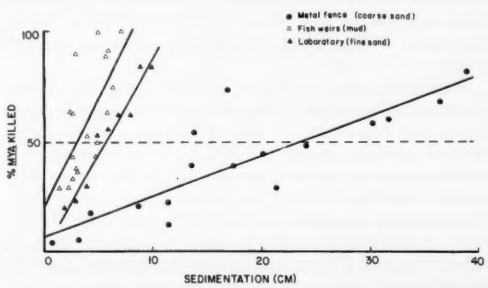

FIG. 2. Mortality of *Mya arenaria* vs. depth of accumulated sediment, for three sediment types. Each regression line is significant and distinct from the others (see text).

TABLE 3. Starting date, ending date, sediment accumulation, accumulation rate, and starting and ending mean densities (with standard deviations) of *Corophium volutator* and *Macoma balthica* for the four boxes in the intertidal mudflat at Mungo Brook. Each mean density is based on a sample size of 4. (*Lower than start, $P < 0.05$, **lower than start, $P < 0.01$, ***mud added by hand.)

Box no.	Starting date	Ending date	Accumulated sediment (cm)	Accumulation rate (cm/mo)	Mean densities (no./m^2)			
					C. volutator		*M. balthica*	
					Start	End	Start	End
1	Aug. 11, 1979	Aug. 23, 1979	2.8***	7.0	16 640	65**	1 453	1 307
					s = 8667	s = 130	s = 171	s = 181
3	Aug. 11, 1979	Aug. 23, 1979	0	0.	17 355	12 740	1 438	1 351
					s = 6948	s = 7366	s = 298	s = 203
8	Aug. 10, 1979	Aug. 23, 1979	1.0	2.3	7 085	4 105*	1 773	1 700
					s = 1048	s = 1802	s = 174	s = 529
9	Aug. 15, 1979	Aug. 22, 1979	2.4***	10.2	5 395	975*	1 831	1 468*
					s = 1349	s = 1781	s = 220	s = 153

dates, sediment samples were taken from each box for comparison with sediment samples taken from the area just before building the boxes.

RESULTS

The four boxes accumulated varying amounts of sediment (Table 3). *Corophium* density decreased significantly in all but box 3 (0 accumulation) (Table 3). A plot of *Corophium* survival vs. depth of accumulated sediment (Fig. 3) shows a clear negative relationship, although sample size is small. There were no changes in *Macoma* density, except for a significant decrease in box 9 (Table 3).

The process of adding mud to two boxes (1 and 9) resulted in increased water content and finer grain sizes (Table 4). There was no change in sediment properties in the boxes to which mud was not added by hand.

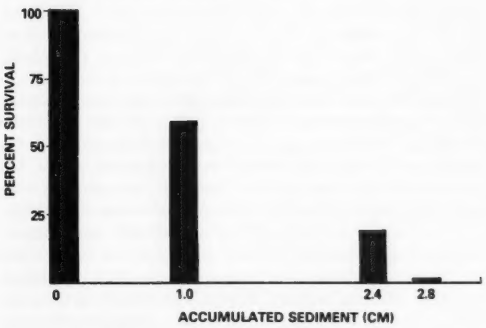

FIG. 3. Survival of *Corophium volutator* vs. depth of accumulated sediment in the four boxes placed in the intertidal mudflat at Mungo Brook. There was no significant change in density in the box with zero accumulation.

Weirs

METHODS

The three weirs sampled were those built and operated by James Webb, Lonzo Webb, and Wayne Linkletter in the Economy Pt. region on the northern shore of Cobequid Bay (Fig. 1). Samples of sediment and fauna were taken from the mud accumulated inside the weirs and from surrounding "natural" sediment. Since there was little difference among the weirs in sediment or fauna, data from all the weirs are lumped for presentation here.

Depth of accumulated mud in the weirs was determined by digging down to the typical surface layer of mixed gravel and mud in several places, and then measuring the depth of the overlying layer of mud. *Macoma* and *Corophium* were sampled in the manner described in the general methods section. Dead and living *M. arenaria* were counted in 0.25-m^2 quadrats. Only *Mya* that appeared to have recently died in place were counted as dead. The valves of these individuals were generally intact and upright, and often still showed signs of recent organic decomposition, such as black reduced sediment.

RESULTS

The relatively hard flats on which the weirs were built had a larger proportion of sand and gravel mixed in with fine sediments than did the mudflats previously discussed. This resulted in larger mean grain sizes and, therefore, lower water contents (Table 5). The sediment that collected behind the weirs was more similar to mudflat sediments, significantly finer and with higher water content than the surrounding flats (Table 5). The mean depth of accumulated mud in the weirs was 5.2 cm (s = 3.56 cm, n = 18). Since these weirs were built around May 1, 1979, and were sampled in mid-August, the rate of accumulation was about 1.5 cm/mo.

Macoma balthica occurred only sporadically and in very low densities in these flats, possibly because the larger grain sizes were not suitable for *Macoma* burrowing and feeding (Yeo 1978). It is therefore difficult to compare quantitatively the natural *Macoma* density of the area to the *Macoma* density in the mud accumulated in the weirs; both were very low. The occurrence of *C. volutator* in these flats was also sporadic, but density was measurable locally, including inside the weirs. In the few places where the mud–gravel mixture of the flats was overlain with several centimetres or more of silt-sized sediments, *Corophium* density was high, with a mean density of

TABLE 4. Water content and mean grain size of the top 2 cm of sediment in the four Mungo Brook boxes on ending dates, and in the same area before boxes were placed (start). Means, standard deviations, and sample sizes are given. (*Different from start, $P < 0.05$, **different from start, $P < 0.005$, otherwise, no change.)

	Water content (% wet wt)		Mean grain size (ϕ)	
Box no.	Start	End	Start	End
1	$\bar{x} = 29.3$, $s = 2.38$, $n = 9$	$\bar{x} = 41.8$**, $s = 4.45$, $n = 2$	$\bar{x} = 5.33$, $s = 0.276$, $n = 5$	$\bar{x} = 6.80$**, $s = 0.130$, $n = 2$
3		$\bar{x} = 30.5$, $s = 0.21$, $n = 2$		$\bar{x} = 5.69$, $s = 0.139$, $n = 2$
8		$\bar{x} = 28.0$, $s = 0.35$, $n = 2$		$\bar{x} = 5.10$, $s = 0.086$, $n = 2$
9		$\bar{x} = 40.2$**, $s = 3.11$, $n = 2$		$\bar{x} = 6.54$*, $s = 0.541$, $n = 2$

TABLE 5. Water content and mean grain size of top 2 cm of sediment accumulated in weirs and of the sediment of the nearby surrounding flats. Mean, standard deviation, and sample size are shown. (*Different from flat sediment, $P < 0.01$.)

	Water content (% wet wt.)	Mean grain size ϕ
Weir sediment	$\bar{x} = 26.0$*, $s = 6.61$, $n = 24$	$\bar{x} = 4.21$*, $s = 0.975$, $n = 10$
Flat sediment	$\bar{x} = 17.2$, $s = 8.89$, $n = 15$	$\bar{x} = 2.76$, $s = 1.022$, $n = 6$

16 349/m^2 (s = 5232/m^2, n = 32). *Corophium* density was also high in weir mud; mean density was 17 961/m^2 (s = 5796/m^2, n = 12) and did not differ significantly from that of the more silty places of the flats.

As at the Selmah fence, the proportion of *Mya* killed was directly and significantly ($P < 0.01$) related to depth of accumulated sediment (Fig. 2, highest regression line), although the depth at which half the population was killed was much smaller, ~3 cm. The regression line for mud (weirs) differs ($P < 0.01$) in slope from the line for coarse sand (Selmah fence). No *Mya* were observed to have burrowed up into the deposited mud.

Laboratory

METHODS

The effect of accumulated fine sand (mean ϕ~3.0) on *M. arenaria* was studied by placing *Mya* at normal depths in fine sand in nine aquaria filled with seawater and well aerated. After ensuring that all *Mya* survived this arrangement, 2–9 cm (depending on aquarium) of the same fine sand was placed on top of the original sediment. The number of *Mya* alive and in each aquarium was determined after 72 h.

RESULTS

As for the weirs and the Selmah fence, the percentage of *Mya* killed was significantly related to the depth of accumulaied sediment (Fig. 2, middle regression line). LD50 was ~6 cm for fine sand. The line for fine sand differs ($P < 0.01$) from the coarse sand (Selmah fence) line in slope and from the mud line (weirs) in elevation. The three lines are thus statistically mutually distinct.

Discussion and Conclusions

COROPHIUM VOLUTATOR

The results from the King Creek fence and the Mungo Brook boxes indicate that a sediment accumulation rate of 2–2½ cm/mo had a devastating effect on the *Corophium* population. The mechanism of this effect is not known. Although the tide would undoubtedly wash many carcasses away, massive mortality of *Corophium* should have been evidenced by the presence of dead individuals; this was not observed. Feeding shorebirds were observed to be not attracted by these structures. Sediment accumulation may have prevented the amphipod from maintaining normal burrows and may thus have resulted in individuals migrating or washing away. If most of these displaced individuals were able to establish themselves elsewhere, then this experiment had little effect on overall *Corophium* abundance in the area. There could be a major adverse effect on the general abundance of *Corophium*, however, if such accumulation were more widespread, as might occur if a tidal dam were built.

A confounding factor at these two sites was change in grain size. The highest *Corophium* densities in Cobequid Bay occur in sediments with mean grain size of 3.5–4.5.ϕ, with density decreasing in coarser and finer sediments (Yeo 1978). The sediment that collected near the King Creek fence had a mean grain size of 3.95ϕ, and so grain size change per se may not be responsible for much of the decrease in *Corophium* density there. The two boxes to which sediment was added, however,

contained sediments of mean grain sizes 6.54ϕ and 6.80ϕ, and the corresponding increased water content may have exaggerated the problem for *Corophium* of constructing and maintaining burrows. The high natural *Corophium* densities near the boxes occurred in sediment with a mean grain size of about 5.3ϕ. The box (8) that accumulated 1.0 cm without sediment being added by hand did not show much change in grain size, but did show a significant decrease in *Corophium* density. The general conclusion is that, although grain size changes are probably partly responsible, sediment accumulation alone had a marked negative effect on *Corophium* density.

The weir results, on the other hand, indicate that an accumulation rate of about 1.5 cm/mo may be sufficiently slow to allow successful recolonization by *Corophium*. An alternative explanation is that the weir accumulation was rapid at first and slow later, thus allowing *Corophium* to colonize later in the absence of rapid accretion.

Macoma balthica

In general, the depths and rates of sediment accumulation in this study were not great enough to affect *Macoma* adversely, although the box with the most rapid accumulation (no. 9) did show a decrease in *Macoma* density. *Macoma* may be able to accommodate moderate accumulation rates by burrowing upward and/or by elongating its siphon to continue feeding on the surface. Greater accumulation rates might significantly affect *Macoma*, and this has been shown to be the case elsewhere (Turk et. al. 1980).

Mya arenaria

Figure 2 shows not only that greater percentages of *Mya* population were killed by deeper accumulations of sediment, but that *Mya* was more sensitive to fine than to coarse sediment. LD50 was ~3 cm for silt, 6 cm for fine sand, and 24 cm for coarse sand. Other studies (Glude 1954; Kranz 1974) have reported mortality of *Mya* as a result of sedimentation. *Mya* is particularly susceptible to sediment deposition due to its loss of burrowing ability with increasing size as a result of declining relative foot size (Kuhl 1972; Schafer 1972). Fine sediments, with their high water content, are probably less amenable to upward burrowing than are coarse sediments, and so have a greater effect on *Mya* when deposited. In the coarse sand at the Selmah fence, many *Mya* of all sizes were found in the layer of accumulated sand. This upward burrowing was not observed in the finer sediments of the laboratory and weirs. In addition, accreting fine sediments may pose a greater siphon-clogging problem for *Mya* than coarse sediment. Other filter-feeding bivalves have been shown to be adversely affected by fine sediments (Rhoads and Young 1970).

Implications for Tidal Power

Higher rates of sediment deposition than measured in this study have been observed in intertidal areas elsewhere in the upper reaches of the Bay of Fundy (Cumberland Basin) (D. C. Gordon, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S., personal communication). We believe, however, that naturally slow rates of deposition and erosion, as measured in this study (Fences — Results) and elsewhere (Yeo 1978) are more typical of the upper reaches at productive times of the year. Erosion rates are often high in the winter because of ice scour and other factors (Knight and Dalrymple 1976), and moderate deposition rates sometimes occur in the spring (Yeo 1978), but infauna generally do not have to contend with significant erosion or deposition during the summer. Storms in this area have been shown to result in rapid erosion and deposition of sediment and in high mortality of infauna (Yeo and Risk 1979b). Such events are relatively uncommon and localized.

A current model of the sedimentary effects of a tidal dam in Cobequid Bay, however, predicts that increased rates of deposition would be widespread (Greenberg 1979). The depth of the deposited sediment would almost certainly exceed the depths observed in this study. Our results show that such deposition (particularly of fine sediment) in areas of Cobequid Bay now supporting populations of *M. arenaria* and *C. volutator* would probably result in large reductions in the density of both species. The consequences for the *Mya* fishery and for the several commercial fish species (Flemming 1979; Gilmurray 1979; Salinas 1979) and migratory shorebird populations (Hicklin 1977; Boates 1979) that feed largely on *Corophium* could be serious. As partial compensation, some areas that now support few *Corophium*, such as the mixed flats containing the weirs, might experience increased *Corophium* density if silt-sized sediment were to accumulate there at a moderate rate.

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A Simple Growth Model for Salmonids in Hatcheries

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IWAMA, G. K., AND A. F. TAUTZ. 1981. A simple growth model for salmonids in hatcheries. Can. J. Fish. Aquat. Sci. 38: 649–656.

A simple growth model for salmonids in hatcheries was developed from several formulations presented in the literature. The model selected was $W_t^{0.33} = W_0^{0.33} + (T/1000)t$ where W_t = weight at time t (g), W_0 = initial weight, T = average temperature (°C), and t = time in days. The model was chosen from a number of possible formulations on the basis of its simplicity. Additional attributes are $W^{0.33}$ is linear with time, the slope of the line $W^{0.33}$ vs. time (termed growth slope) is linear with temperature (i.e. $T/1000$) over the temperature range commonly found in hatcheries that rear salmonids, and $W^{0.33}$ is easily converted to length. Tests of the model on wild stock steelhead in British Columbia hatcheries provided good results under normal operating conditions of feeding, loading, etc. Applications of the model are also presented, including the development of a growth coefficient allowing comparisons of growth rate corrected for fish size and temperature effects.

Key words: growth model, salmonids, fish culture

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Des formules extraites de diverses publications ont servi à construire le modèle de croissance simple pour salmonidés d'élevage décrit dans l'article qui suit. Le modèle choisi est le suivant : $W_0^{0.33} = W_0^{0.33} + (T/1000)t$, où W_t = le poids au temps (g); W_0 = le poids initial; T = la température moyenne (°C); et t = le temps en jours. C'est à cause de sa simplicité que nous avons choisi ce modèle parmi plusieurs. Les attributs supplémentaires sont : $W^{0,33}$ est linéaire en fonction du temps; la pente de la ligne $W^{0,33}$ vs. temps (appelée pente de croissance) est linéaire en fonction de la température (i.e. $T/1000$) dans la gamme de températures communément rencontrées dans les établissements salmonicoles, et $W^{0,33}$ peut facilement se convertir en longueur. Des essais du modèle sur un stock sauvage de truites steelhead dans des piscicultures de Colombie-Britannique donnèrent de bons résultats dans des conditions normales d'opération, alimentation, charge, etc. Nous présentons également des applications de ce modèle, y compris un coefficient de croissance permettant de comparer des taux de croissance « corrigés » pour tenir compte de la taille des poissons et des effets de la température.

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A mathematical model of fish growth has several important applications in fisheries management, yet, despite many attempts to develop mathematical analogs of growth, there exists a large diversity of approaches and concepts. It is common to find growth expressed as centimetres per month, instantaneous growth rates, percentage of change in length, or percentage of change in weight, often without reference to temperatures, ration, or cultural conditions. In anadromous fish culture, the problem of predicting size as a function of time, ration, and temperature is of particular importance since parr–smolt transformation is size dependent in some species (Wagner 1971) and ocean survival appears to be influenced by size and time of release (Wallis 1968; Bardach and Ryther 1968; Cleaver 1969; Johnson 1970; Royal 1972). Practical growth models are also of significance in the design of new facilities and in the rescheduling of production targets to meet changing management priorities.

The purpose of the present paper is to examine existing concepts of growth as they pertain to the development of a rule-of-thumb approach to predicting growth in hatcheries under normal operating conditions, and to describe a possible method of comparing growth rates of fish of various sizes reared at various temperatures.

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Existing Models of Growth

During the life history of a fish, periods or stanzas of undisturbed growth are often marked by physiological or ecological size thresholds such as smoltification and availability of prey organisms. Parker and Larkin (1959) suggest that within each of these growth stanzas, growth rate (dW/dt) can be described as a power of W, i.e.

$$(1)\quad \frac{dW}{dt} = KW^x$$

This formulation describes several physiological rate processes related to size, with the consequence that weight gain per day increases as a function of size, but declines when measured as a percentage increase per day, i.e. specific growth rate. Thus, given adequate rearing conditions and constant temperatures, one would expect specific growth rate to be maximum in the early life history and continually decline thereafter. Brett et al. (1969) working with sockeye salmon (*Oncorhynchus nerka*) and Elliott (1975) working with brown trout (*Salmo trutta*) have examined the relationship between specific growth rate and fish size. Both authors suggest that a linear negative relationship exists between specific growth rate and body weight, given a logarithmic transformation of the data. In addition, it appears that the slope of the above relationship is relatively constant for different temperatures. Thus, the effect of temperature is to determine the intercept of the line relating specific growth rate to body size, with the overall result producing a family of lines relating growth rate to weight and temperature (Fig. 1).

Given that the experimental evidence tends to support the concept that dW/dt is some function of weight, it is desirable

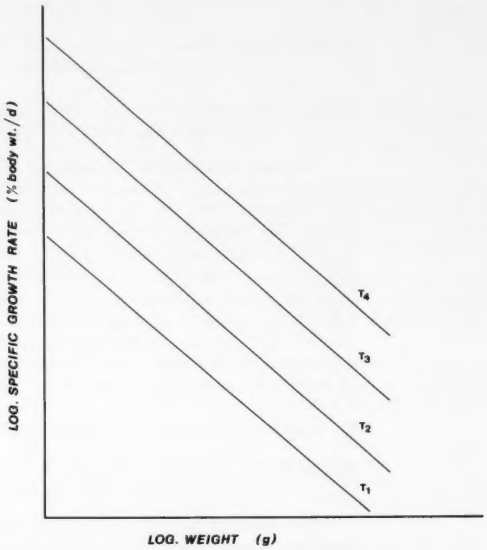

FIG. 1. General relationship between specific growth rate and weight (logarithmic axes) for a series of temperatures ($T1-T4$).

TABLE 1. Comparison of growth model coefficients for a variety of species and conditions.

Source	Species	Temp.	(x) $dW/dt = kW^x$	(b) $W_t^b = W_0^b + tG_s$	Comments
Parker and Larkin 1959	Steelhead	—	0.80	0.20	Measured from adult scales, 3/1 life history
Parker and Larkin 1959	Steelhead	—	0.67	0.33	Measured from adult scales, 2/2 life history
Parker and Larkin 1959	Chinook	—	0.56	0.44	Measured from adult scales, 0/3 life history
Parker and Larkin 1959	Chinook	—	0.57	0.43	Measured from adult scales, 0/4 life history
Parker and Larkin 1959	Chinook	—	0.63	0.37	Measured from adult scales, 0/5 life history
Parker and Larkin 1959	—	—	0.73	0.27	Theoretical metabolic rate increase
Haskell 1948	Brook trout	11.0	0.67	0.33	Hatchery, 1.5–60 g
Cooper 1961	Brook trout (wild)	10.0	0.50	0.50	Hatchery, 2.5–350 g
Cooper 1961	Brook trout (inbred)	10.0	0.60	0.40	Hatchery, 2.5–350 g
Brett 1974	Sockeye salmon	15.0	0.51	0.49	Laboratory, 6–70 g
Brett 1974	Pink salmon	15.0	0.55	0.45	Laboratory, 5–60 g
Brett 1974	Sockeye salmon	15.5	0.60	0.40	Laboratory, 0.3–75 g
Brett 1974	Sockeye salmon	10.5	0.61	0.39	Laboratory, 0.3–75 g
Stauffer 1973	Coho salmon	15.5	0.66	0.34	From Haskell, but good for hatchery coho
Brett and Shelbourn 1975	Sockeye salmon	15.0	0.58	0.42	Laboratory, 3–45 g
Elliott 1975	Brown trout	5.6	0.67	0.33	Laboratory, 10–300 g
Elliott 1975	Brown trout	9.5	0.67	0.33	Laboratory, 10–300 g
Elliott 1975	Brown trout	12.8	0.68	0.32	Laboratory, 10–300 g
Elliott 1975	Brown trout	15.0	0.69	0.31	Laboratory, 10–300 g
Elliott 1975	Brown trout	19.5	0.72	0.28	Laboratory, 10–300 g
Overall mean			0.63	0.37	

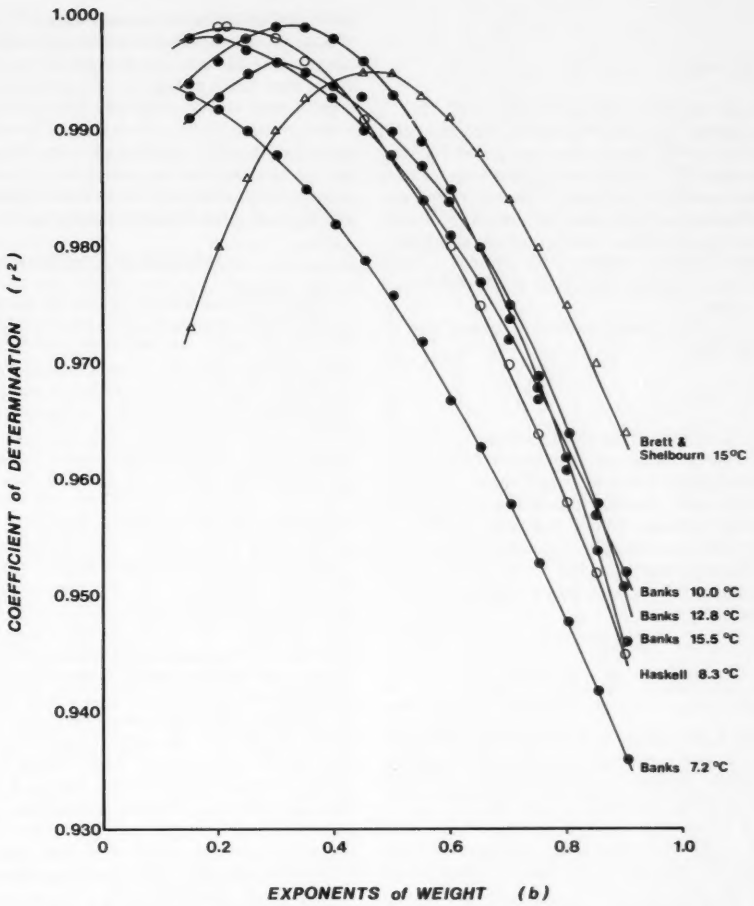

FIG. 2. Coefficients of determination (r^2) for various exponents (b) of weight (W) in linear regressions of W^b on time for data from several studies.

to obtain an explicit solution for weight. Rearranging and integrating equation (1)

$$(2) \quad \int_{W_0}^{W_t} W^{-X}\, dW = K \int_0^t dt$$

yields

$$(3) \quad W_t^{(1-X)} = W_0^{(1-X)} + K\,(1-X)t.$$

In their analysis of steelhead life history, Parker and Larkin (1959) conclude that the exponent of weight was in the order of 0.20 ($X = 0.8$). Thus

$$(4) \quad W_t^{0.20} = W_0^{0.20} + ct$$

is the predictive form of equation (1) where t = time in days and c is a constant related to the growth characteristics of the species in terms of temperature and ration. However, considerable variation was also noted and the weight exponent was observed to vary from 0.17 to 0.50.

Paloheimo and Dickie (1965) using other assumptions derived a formulation which was identical with the Parker and Larkin (1959) equation under specified conditions. They too suggested that a theoretical case could be made for predicting weight at time t as a function of $W^{0.20}$ but also concluded that exponents higher than 0.20 may be the rule rather than the exception. Cooper (1961) using the same type of analysis as Parker and Larkin (1959) compared growth coefficients for wild and hatchery strains of brook trout (*Salvelinus fontinalis*) and concluded that the exponent of weight ranged from 0.5 for randomly bred fish to 0.4 for inbred strains. Elliott (1975) working with brown trout developed a predictive equation which was tested experimentally and found to give estimates of within ±4.0% for fish within the 10- to 300-g range. His

equation

$$(5)\quad W_t^{b_1} = W_0^{b_1} + Kt$$

used exponents of weight (b_1) between 0.279 and 0.325.

In the more applied fish culture literature, Haskell (1948) and later Stauffer (1973) found what appears to be good predictive fits when $W^{0.33}$ was plotted against time for constant temperatures and maximum rations. Haskell's work was conducted with brook trout while Stauffer worked on a model of coho salmon (*Oncorhynchus kisutch*) growth in hatchery situations. Banks (1981), working with chinook salmon (*Oncorhynchus tshawytscha*), also used weight $W^{0.33}$ with considerable success.

In general, all of the above models of growth can be expressed in the form

$$(6)\quad W_t^b = W_0^b + G_s t$$

where b is the exponent of weight which results in a linear plot of W^b vs. time, and G_s (which we term growth slope) is the slope of the line. Models which use length increase per unit time reduce to the above equation if there is a cubic or near cubic relationship between length and weight. Specific growth rate also reduces to the above formulation, but in a less obvious way. Recognizing again that (6) is the integrated form of equation (1), dividing each side of equation (1) by W and taking logarithms yields

$$(7)\quad \log \frac{dW}{dt} \Big/ W = \log K + (X - 1) \log W.$$

Since $(dW/dt)/W$ is the change in weight per day divided by the initial weight, the expression is equivalent to specific growth rate. Further, the slope of the line relating log specific growth rate to weight is equal to $X - 1$ or $-b$.

As a result of the above analysis, it is possible to compare many different sets of data found in the literature (Table 1). Values of b generally ranged from 0.20 to 0.50. High values were observed for pink salmon (*Oncorhynchus gorbuscha*) and wild brook trout whereas rainbow trout (steelhead) (*Salmo gairdneri*) and brown trout appeared to represent the lower end of the scale. The interpretation of these differences is not clear and is perhaps an area for future research. However, it must also be noted that while the table summarizes values presented in the various papers, the data are not necessarily the "best fit" values in all cases. For present purposes we can conclude that the various theoretical descriptions of growth are consistent and that practical predictions of growth can be made given appropriate measures of b and G_s.

Selection of Coefficients

Criteria for the selection of values for the coefficients b and G_s are of some importance given the normal large variation in growth data and a two-parameter model. In describing the characteristics of K and X (equation (1)) Parker and Larkin (1959) speculated that X is related to genetically controlled physiological processes while K measured ecological opportunities. In the present discussion, b (i.e. $1 - X$) is the exponent of weight, such that when a series of successive values of W^b is plotted against time, a straight line is obtained with slope G_s (i.e. K). This slope is also a function of ration size, temperature, or other ecological factors.

The range of b values calculated from the literature (Table 1) suggested that weight predictions may be relatively insensitive to values of the exponent b. This was tested by calculating coefficients of determination (r^2) for linear regression equations of $W_t^b = W_0^b + G_s t$ for 100 values of b from 0.01 to 1.00 for several sets of data; i.e. $W^{0.01}, W^{0.02} \ldots W^{1.0}$. Values were regressed against time and the resulting r^2 values plotted against the values of b (Fig. 2). As would be expected all equations gave high values of r^2 but in most cases a dome-shaped curve was suggested, peaking between values of b ranging from 0.19 to 0.45. Not all data showed this tendency, however, and in some cases (e.g. Elliott 1975) no consistent pattern of r^2 values was evident. A summary of b values giving maximum r^2 for selected data (Table 2) suggests that within a species at least, r^2 was not sensitive to values of b within the range 0.20−0.40, and in some cases even larger ranges may be tolerated.

TABLE 2. The b values that resulted in the best linear fit of W^b to time in the linear regression analyses of experimental data from several sources.

Data source	Species	Rearing temp. °C	b	r^2
Brett and Shelbourn (1975)	Sockeye salmon	15.0	0.45	0.99502
Banks (1981)	Chinook salmon	10.0	0.19	0.99785
		12.8	0.31	0.99536
		15.5	0.31	0.99926
Elliott (1975)	Brown trout	5.6	0.28	0.99989
		7.1	0.29	0.99279
		9.5	0.27	0.99734
Haskell (1948)	Brook trout	8.3	0.21	0.99867
Range		(5.6−15.5)	(1.19−0.45)	(0.99279−0.99989)

With regard to the second parameter in the equation, Elliott (1975) suggested that G_s should be a linear function of temperature (T),

$$(8) \quad G_s = -0.003 + 0.0009\,T°C \qquad (3.8 \leq T \leq 12.8).$$

Haskell et al. (1956) also reported that a linear relationship existed between G_s and T in groups of brook trout of the same stock reared at eight different hatcheries. From a pragmatic point of view, a linear relationship between G_s and T must be considered desirable since this allows for the use of accumulated temperature units and/or average temperature in growth prediction models. Nonlinear temperature models can be considered only for those with access to computers or with greater interest in the mechanisms rather than the prediction of growth.

If G_s is approximately a linear function of temperature over a specified range of temperatures, an additional constraint is imposed on the selection of predictive values of b and G_s. Thus, the two conditions to be satisfied are (1) that W^b vs. time be linear, and (2) that G_s is linear with T over the normal range of operating temperatures in salmonid hatcheries (4°C−18°C).

Existing data were examined in the above context to determine the relationship between the selection of b and the linearity of G_s with T. Bank's (1981) data on chinook salmon growth were examined first by regressing a wide variety of b values against time to obtain a series of G_s values. Each set of G_s values associated with a particular b value was then regressed against temperature (T) to determine the best linear fit. In the analysis, $b = 0.55$ provided the best linear fit for G_s and T, but what was perhaps more interesting was the lack of sensitivity of the analysis to the value selected for b. For example, for $b = 0.60$, the r^2 value of G_s on T was 0.994; for $b = 0.20$, r^2 was 0.988 (Fig. 3). Examination of other data also suggested an insensitivity to the selection of b values. Elliott's (1975) data indicated that a b value of 0.03 gave the best linear fit of G_s to T while the data of Brett et al. (1969) indicated a b value of 0.98. It is important to note again, however, that there were only slight differences in the r^2 values over the range of b's selected, and that in the case of the latter two values, even though they provided a linear fit of G_s on T, they did not provide linear fits of W^b on time. One can conclude therefore, that the available data are not sufficient to distinguish among several possible combinations of b and G_s, or perhaps more to the point, several combinations of b and G_s give acceptably good predictions of growth as a function of initial weight, time, and temperature.

For practical purposes we were willing to trade off some accuracy to gain simplicity, and the problem became one of identifying which of the possible values of b and G_s resulted in the simplest model. Examination of the data indicated that for some values of b, G_s was equal to temperature (T°C) ÷ 1000, and further, that these values of b were within the range of desirable (linear) b values (0.20−0.40). Consequently it was possible to select the value of b by determining which of the G_s values was equal to $T \div 1000$, i.e. the data were analyzed again to determine which value of b was associated with the best linear fit of G_s to $T/1000$ (Table 3). It was a convenient coincidence that these b values were all within the linear range specified earlier and that three of the four were near 0.333. This was particularly useful because of the convertibility of $W^{0.33}$ and length as well as the previously demonstrated good fits of $W^{0.33}$ vs. time. Using $W^{0.33}$ there-

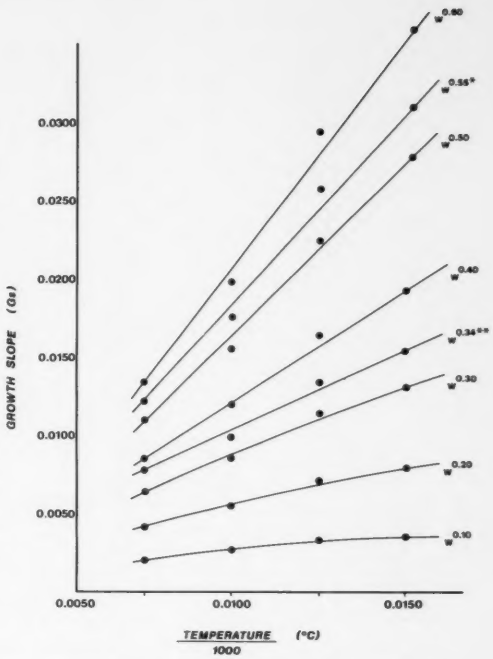

FIG. 3. An example of the effect of altering the weight exponent value (b) on the relationship between G_s and T. Data from chinook salmon (Banks 1971).

TABLE 3. Results of linear regression analysis of G_s on $T/1000$ for several W^b vs. time data sets. Only the b value associated with the best fit, i.e. slope = 1, maximum r^2, is presented.

Data source	Species	b	r^2	Slope	Size range (g)	T range (°C)
Shelbourn et al. (1973)	Sockeye	0.20	0.987	1.005	0.4−4.4	5.0−15.0
Brett et al. (1969)	Sockeye	0.33	0.968	1.042	1.2−85.5	4.8−14.9
Elliott (1975)	Brown trout	0.30	0.980	1.041	50.0−62.0	5.6−15.0
Banks (1981)	Chinook	0.34	0.992	1.003	0.4−10.4	7.2−15.6

fore resulted in a model of the form

$$W_t^{0.33} = W_0^{0.33} + (T/1000)t$$

which has the following attributes:

1) $W^{0.33}$ vs. time is linear
2) G_s is a simple function of temperature (T/1000) and is linear with temperature over most of the temperature ranges found in hatcheries rearing salmonids
3) $W^{0.33}$ and length are easily convertible.

A model using $W^{0.33}$ was fitted to existing data (Fig. 4) as well as to data from our own hatchery system, with acceptable results (Table 4). Further work is continuing to determine the limitations of the model since it clearly does not include other factors which influence growth such as rearing density, genetic stock, and feeding schedule. Nevertheless, preliminary indications are that the model quite often gives predictions within ±10−20% of final weight on our wild stock rainbow

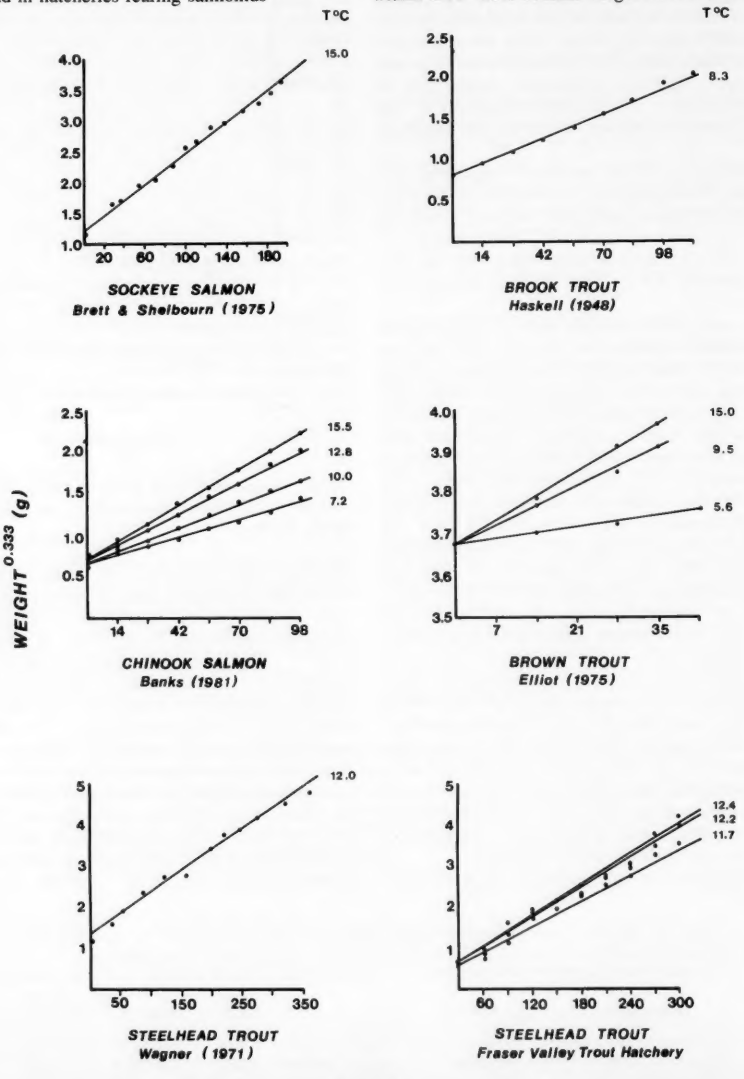

FIG. 4. Weight$^{0.333}$ vs. time for a variety of species of salmonids and temperatures.

populations when reared in hatcheries.

Application of the Model

Assuming that G_s describes growth for a particular group of fish, it is then possible to compare fish at different sizes grown at different temperatures, with a coefficient (G_c) calculated as $(G_s \times 1000)/T$. This coefficient is 1.0 if a particular group of fish is growing according to the model, whereas values above or below 1.0 indicate better or poorer growth, respectively.

TABLE 4. Summary of linear regression[a] analyses of steelhead trout growth data from various hatcheries in British Columbia.

Source	Production year	n	Avg. daily temp. (°C)	Growth slope (G_s)	Coeff. of determ. (r^2)
Fraser Valley Trout Hatchery					
Qualicum R. stock	1978 79	8	13.0	0.0130	0.9900
Alouette R. stock	1978 79	7	13.0	0.0130	0.9610
Fraser Valley Research Facility					
Vedder R. stock	1977 78	5	11.3	0.0123	0.9951
Vedder R. stock	1978 79	13	12.0	0.0127	0.9944
Robertson Creek Hatchery					
Robertson Cr. stock	1975 76	7	15.9	0.0143	0.9982
Robertson Cr. stock	1977 78	10	18.0	0.0175	0.9954
Quinsam River Hatchery					
Quinsam R. stock	1976 77	9	10.9	0.0104	0.9925
Qualicum River Hatchery					
Quinsam R. stock	1974 75	4	12.0	0.0121	0.9944
Capilano River Hatchery					
Capilano R. stock	1972 73	14	9.9	0.0091	0.9940
Capilano R. stock	1973 74	13	9.3	0.0087	0.9894
Capilano R. stock	1974 75	7	8.7	0.0085	0.9936

[a]Regressions of $W_t^{0.33}$ on rearing time.

TABLE 5. Growth coefficients (G_c) for various stocks of salmonids. $G_c = (G_s \times 1000) \div T$°C.

Species	Source[a]			Avg. T°C	G_c
Steelhead trout	FVTH	Qualicum stock	1978/79	13.0	1.000
Steelhead trout	FVTH	Alouette stock	1978/79	13.0	1.000
Steelhead trout	FVTH	Vedder stock	1977/78	11.3	1.089
Steelhead trout	FVTH	Vedder stock	1978/79	12.0	1.058
Steelhead trout	RCH	Robertson stock	1975/76	15.9	0.899
Steelhead trout	RCH	Robertson stock	1977/78	18.0	0.972
Steelhead trout	QURH	Quinsam stock	1976/77	10.9	0.954
Steelhead trout	QLRH	Qualicum stock	1974/75	12.0	1.008
Steelhead trout	CRH	Capilano stock	1972/73	9.9	0.919
Steelhead trout	CRH	Capilano stock	1973/74	9.3	0.936
Steelhead trout	CRH	Capilano stock	1974/75	8.7	0.977
Brook trout	Haskell (1948)			8.3	1.289
Brown trout	Elliott (1975)			15.0	0.533
Brown trout	Elliott (1975)			9.5	0.695
Brown trout	Elliott (1975)			5.6	0.304
Sockeye salmon	Brett and Shelbourn (1975)			15.0	0.840
Chinook salmon	Banks (1981)			15.5	0.955
Chinook salmon	Banks (1981)			12.8	0.984
Chinook salmon	Banks (1981)			10.0	0.930
Chinook salmon	Banks (1981)			7.2	0.972

[a]FTVH, Fraser Valley Trout Hatchery; RCH, Robertson Creek Hatchery; QURH, Quinsam River Hatchery; QLRH, Qualicum River Hatchery; CRH, Capilano River Hatchery.

The growth coefficients for several stocks of salmonids reared at average temperatures from 5.6 to 18.0°C are listed in Table 5. The coefficients indicate that after adjusting for fish size and temperature, brook trout in Haskell's study grew "better" than any of the other species followed by the steelhead trout in the British Columbia hatcheries. The growth coefficients may reflect the effects of site- or stock-specific factors on growth. For example, it seems that within the steelhead trout reared in British Columbia, high temperatures or other site-specific factors at Robertson Creek hatchery tended to depress the growth of this species below the values for other sites. Furthermore, the growth of brown trout seems to be lower, in general, compared to the other species of salmonids in this table. Thus, this coefficient may be useful in monitoring the growth of a single species, comparing growth among different species within a hatchery, or, in some cases, between hatcheries.

Practical applications of the predictive model where $b = 0.333$, and $G_s = T°C/1000$ are presented below by solving several growth-related problems that arise in routine fish culture.

1) Weight prediction: Predict the final average weight of a 5-g fish after 100 d of rearing at the following daily temperatures: 32 d at 10°C; 45 d at 13°C; 17 d at 8°C; and 6 d at 6°C.

$$\text{Average water temperature} = \frac{32(10) + 45(13) + 17(8) + 6(6)}{100} = 10.8°C$$

$$G_s = \frac{T°C}{1000} = \frac{10.8}{1000} = 0.0108.$$

$$\text{Final weight} = W_t = (W_0^{0.33} + G_s t)^3 = [1.71 + 0.0108\ (100)]^3 = 21.72 \text{ g}.$$

2) Time prediction: Predict the time required to raise 7 g fish to 55 g with an average daily water temperature of 10.0°C.

$$G_s = \frac{T°C}{1000} = \frac{10}{1000} = 0.0100$$

$$t = \frac{W_t^{0.33} - W_0^{0.33}}{t} = \frac{3.80 - 1.91}{0.0100} = 189 \text{ d}.$$

3) Temperature prediction: What average daily temperature is required to raise a 5-g fish to 55 g in 180 d?

$$G_s = \frac{W_t^{0.33} - W_0^{0.33}}{t} = \frac{3.80 - 1.91}{180} = 0.0116.$$

$$T = G_s \times 1000 = 0.0116 \times 1000 = 11.6°C.$$

More research in fish growth is required where growth data at various temperatures over time is reported along with detailed rearing conditions. Such data would enable a better resolution of the relationship between G_s and T for various species and families of fishes and also provide further data on effects of such factors as loading rate on growth. Furthermore, the intercept and slope of the line relating G_s and T may reveal important and useful information regarding the physiological nature of growth in various fishes.

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Optimum Size Limits for Trout Fisheries

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JENSEN, A. L. 1981. Optimum size limits for trout fisheries. Can. J. Fish. Aquat. Sci. 38: 657–661.

Application of conventional stock assessment methods to total catch of sport fisheries give neither optimum size limits nor optimum effort; as size limits decrease and effort increases total yield increases asymptotically. In this study total catch is separated into non-trophy and trophy catch; trophy catch has an optimum with respect to fishing effort. Increasing trophy catch decreases total catch, so to optimize the fishery a value is assigned to each category of catch. Optimum size limits for both conventional and slot limits are examined. A slot limit attempts to increase trophy catch without causing a substantial decrease in total catch. Fish are illegal until they reach some minimum size, then they are legal until they reach a certain size or age. They are then again illegal until they reach a trophy size. The results indicate recruitment age should be the smallest size acceptable to fishermen unless trophy fish have a very high value. With conventional size limits total catch decreases rapidly as age at entry increases and fishing effort decreases. Optimum slot limits are determined; slot limits produce a small increase in trophy catch and do not cause a large decrease in total catch.

Key words: slot limits, trout fisheries, sport fisheries management, trophy catch

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Les méthodes conventionnelles d'évaluation des stocks appliquées qux prises totales de la pêche sportive ne donnent pas les limites de taille optimales, non plus que l'effort optimum. À mesure que les limites de taille diminuent et que l'effort augmente, le rendement total croît asymptotiquement. Dans l'étude décrite ci-dessous, nous avons séparé les prises en deux groupes: non trophée et trophée; les prises-trophées ont un optimum par rapport à l'effort de pêche. Une augmentation des prises-trophées entraîne une diminution des prises totales. C'est pourquoi nous assignons une valeur à chaque catégorie de prises, afin d'optimiser la pêche. Nous examinons les limites de taille optimales, tant conventionnelles que par tranches. Une limite par tranches vise à augmenter les prises-trophées sans causer de diminution substantielle des prises totales. La capture des poissons est illégale tant que ces derniers n'auront pas atteint une taille minimale quelconque, elle est ensuite légale jusqu'à ce qu'ils atteignent une certaine taille ou âge. La capture devient de nouveau illégale jusqu'à ce qu'ils aient atteint une taille de trophée. Les résultats indiquent que l'âge du recrutement devrait correspondre à la plus petite taille acceptable aux pêcheurs, à moins que les poissons-trophées aient une très haute valeur. Avec des limites de taille conventionnelles, les prises totales diminuent rapidement à mesure qu'augmente l'âge d'arrivée dans la phase pêchable et que diminue l'effort de pêche. Nous déterminons les limites par tranches; ces dernières donnent une faible augmentation des prises-trophées et ne causent pas d'importante diminution des prises totales.

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REGULATION of fisheries requires an understanding of stock dynamics so that the impact of regulations can be predicted. Some of this necessary understanding can be provided by mathematical models. Stock assessment models have been widely applied for management of commercial fisheries, but such models have seldom been applied for management of sport fisheries. Ricker (1945), Jensen (1976), and Allen (1955a, b) applied analytical models to examine the impact on catches of changes in length at entry and bag limits. No optimum conditions for management were discovered and this might be a major reason why little interest developed in application of these models to sport fisheries. As the age at entry increases and bag limits decrease, total catch decreases; when dealing with total catch in numbers there is no optimum yield as a function of effort or age at entry.

In this study total catch is separated into a trophy catch and a non-trophy catch and the impact on total and trophy catch of change in age at entry into the fishery and change in fishing mortality are examined with conventional size limits and slot limits. Overfishing does not occur if only total catch is considered, but if the catch is separated into total catch and trophy

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catch the relation between trophy catch and fishing mortality has a maximum, and overfishing can be defined as a level of fishing that reduces the trophy catch below the maximum level. Management to increase trophy catch causes a decrease in total catch, and one approach to obtain an optimum level of fishing is to assign a value to each category of catch; then the conditions that give a maximum value for the fishery can be obtained. The units assigned to value might be dollars or any relative measure of value. The objective of this study is to develop and apply some general management concepts rather than to develop a detailed program for regulation of a particular fishery.

Model Development

The change in catch from a cohort and the change in the size of the cohort with respect to age can be modeled with the equations

$$\frac{dC}{dx} = FN$$

$$(1)\quad \frac{dN}{dx} = -MN,\ x_r < x < x_c$$

$$\frac{dN}{dx} = -(F + M)N,\ x > x_c$$

where: F = instantaneous fishing mortality coefficient, M = instantaneous natural mortality coefficient, N = size of cohort in numbers, C = catch in number, x_c = age at entry into the exploited stock, x_r = age at which fish could be recruited.

The above model is the same as the model applied by Allen (1955a, b). In application of this model it is assumed that there is no growth compensation. Allen has examined this assumption in detail. Growth compensation does occur, but it should be a serious problem only with conventional size limits. It also will be assumed that illegal-sized fish caught and released suffer no hooking mortality since hooking mortality in fly-fishing areas is small.

The model examines only changes in age structure that occur with different sizes at entry regulations. Favro et al. (1979, 1980) have suggested that genetic changes occur under selective fishing. Most biologists probably would agree that such changes are possible, but there is little evidence that the genetic changes postulated by Favro et al. have occurred in the State of Michigan trout streams (Clark et al. 1980).

Applying equation (1) gives the total catch per recruit as

$$(2)\quad C_{tot} = \frac{FRe^{-M(x_c - x_r)}}{F + M}$$

where R is the number of recruits or individuals of age x_r. The catch of trophy fish is found by integration of equations (1) from x_{tr}, where x_{tr} is the age when fish become trophy fish. The result is

$$(3)\quad C_{tr} = \frac{FRe^{-M(x_c - x_r) - (F + M)(x_{tr} - x_c)}}{F + M}.$$

Total catch from the fishery increases toward an asymptote as F increases, and the value of the asymptote depends on the age at which the fish are first vulnerable to capture. Trophy catch on the other hand increases to a maximum and then begins to decrease as F increases for $x_c < x_{tr}$. The level of F that produces the maximum trophy catch and the maximum trophy catch itself are both functions of the age when the fish become vulnerable. The level of fishing that produces the maximum catch of trophy fish can be found from equation (3) and is

$$(4)\quad F = \frac{-M(x_{tr} - x_c) + \sqrt{M^2(x_{tr} - x_c)^2 + 4M(x_{tr} - x_c)}}{2(x_{tr} - x_c)}.$$

Slot limits have been proposed as a method to produce and maintain quality fishing without severely reducing the total catch. Fish are illegal until they reach some minimum size, then they are legal until they reach a certain size. They are then again illegal until they reach a trophy size. Let l_c, l_f, and l_{tr} be lengths such that $l_c < l_f < l_{tr}$, and l_c is a minimum length acceptable to fishermen, and l_{tr} is a trophy length. In slot limits fish are illegal up to size l_c, legal from size l_c to l_f, illegal from size l_f to l_{tr}, and then legal again after length l_{tr}. For a fishery that is regulated with a slot limit the model for catch and change in cohort size with respect to age becomes

$$\frac{dC}{dx} = FN$$

$$(5)\quad \frac{dN}{dx} = -MN,\ x_r < x < x_c \text{ and } x_f < x < x_{tr}$$

$$\frac{dN}{dx} = -(F + M)N,\ x_c < x < x_f \text{ and } x > x_{tr}$$

where x_f is the age at which legal fish again become illegal. Natural mortality alone operates between ages x_r and x_c and between ages x_f and x_{tr}. Both natural and fishing mortality operate between ages x_c and x_f and after age x_{tr}. More complex mortality schedules can be examined, but they result in a more complex model, and the above model captures the key features of slot limits.

Integration of equation (5) gives the trophy catch, C_{tr}, as

$$(6)\quad C_{tr} = \frac{FRe^{-M(x_c - x_r) - (F + M)(x_f - x_c) - M(x_{tr} - x_f)}}{F + M}$$

and the non-trophy catch, C_{nt}, as

$$(7)\quad C_{nt} = \frac{FRe^{-M(x_c - x_r)}}{F + M}(1 - e^{-(F + M)(x_f - x_c)}).$$

Total catch is $C_{tot} = C_{tr} + C_{nt}$. For fixed values of M, x_f, and x_c, the maximum trophy catch is obtained with

$$(8)\quad F = \frac{-M(x_f - x_c) + \sqrt{M^2(x_f - x_c)^2 + 4M(x_f - x_c)}}{2(x_f - x_c)}.$$

Increasing trophy catch by changing x_c or F results in a large decrease in total catch but large fish which have trophy value might be considered of higher value than smaller fish. The objective in management of a sport fishery might be to obtain the maximum total value where the total value is the sum of the value of trophy and non-trophy fish, i.e.

$$(9) \quad V_{tot} = C_{nt}V_{nt} + C_{tr}V_{tr}$$

where V_{nt} is the value of a non-trophy fish and V_{tr} is the value of a trophy fish. Value can be measured in dollars or any relative measure of value.

For a fishery without a slot limit the total value is a function of the age at entry into the fishery, x_c. Substitution of the solutions for the catch equations into equation (9) and application of calculus shows that a minimum value of the total catch occurs when

$$(10) \quad x_c = x_{tr} + \frac{1}{F + M} \ln\left[\frac{MV_{nt}}{F(V_{tr} - V_{nt})}\right].$$

The value of the catch is high when x_c is small; the value decreases to a minimum as x_c is increased and then the value begins to increase as x_c is increased further.

If a slot limit is applied the total value of the yield from the fishery will change with change in both x_c and x_f. In this case application of calculus shows that a maximum value occurs where

$$(11) \quad x_f = x_{tr} + \frac{1}{M} \ln\left[\frac{(F + M)V_{nt}}{FV_{tr}}\right]$$

and a minimum value occurs where

$$(12) \quad x_c = x_f + \frac{1}{F + M} \ln\left[\frac{MV_{nt}}{F(V_{tr}e^{-M(x_{tr} - x_f)} - V_{nt})}\right].$$

The value of x_f does not depend on x_c. These equations can be applied either to determine the ages x_f and x_c that maximize total value or, given that x_f and x_c have been established by some alternative approach, these equations can be applied to calculate the relative value implicitly assigned to trophy and non-trophy fish.

Application to Lawrence Creek Brook Trout

The above models are applied to examine the likely impact of different management regulations using data for brook trout (*Salvelinus fontinalis*) fishery on Lawrence Creek, Wisconsin. Good estimates of growth and mortality are available for the Lawrence Creek population (McFadden 1961) and impacts of conventional size and bag regulations have been studied experimentally by Hunt et al. (1962).

The average size of brook trout of different ages in Lawrence Creek and some general average size data are listed in Table 1. The models were applied using age as the criterion for regulation under the assumption that size at age is given in Table 1, and that age can be readily converted to size. The natural mortality coefficient for Lawrence Creek brook trout is about $M = 0.70$ and the fishing mortality coefficient is about $F = 0.50$ (McFadden 1961). It was assumed that trophy fish are fish of age 4 and older, that is, fish larger than 33.02 cm in length.

TABLE 1. Lengths (cm) at age of brook trout (*Salvelinus fontinalis*) generally and for Lawrence Creek.

Age	Average length[a]	Lawrence Creek[b]
1	15.49	17.02
2	19.58	20.83
3	24.08	29.21
4	32.31	35.31
5	36.80	36.58

[a]Carlander (1969).
[b]McFadden (1961).

First the impact on the total catch and trophy catch of changes in age at entry to the fishery and changes in the fishing mortality coefficient will be examined using conventional size limits. Total catch increases asymptotically as F increases and the level of the asymptote is determined by x_c (Fig. 1). Increasing x_c from age 1 to age 2 decreases total catch by nearly 50% (Fig. 1) and with $F = 0.50$ it increases trophy catch only by about 40%. For example, with $R = 1000$ and $F = 0.50$, changing x_c from age 1 to age 2 decreases total catch from 417 to 207 and increases trophy catch from 11 to 19. If F is small, increasing x_c from age 1 to age 2 still decreases total catch about 50% but increases trophy catch by less than 25%.

To calculate the total value of the fishery with conventional size limits I assigned non-trophy fish a value of 1 unit and trophy fish values of 5, 10, and 15 units. In all cases the total value of the catch decreases to a minimum and then begins to increase as x_c increases (Fig. 2). As the value of a trophy fish increases, the minimum total value of the catch is reached with the age of entry at younger ages. If the value of a trophy fish is high enough, the maximum value of the catch occurs with $x_c = x_{tr}$, i.e. the legal size should be increased to the trophy size. Increasing x_c to increase trophy catch can be justified only when a high value is placed on trophy catch and then x_c should be increased to x_{tr}.

As F increases trophy catch increases to a maximum and

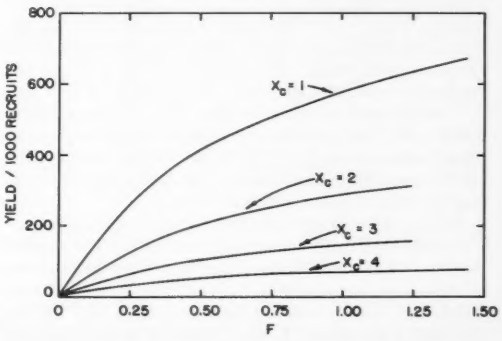

FIG. 1. Total yield per 1000 recruits as a function of fishing mortality with different ages of entry into the exploited population, x_c, and conventional size limits.

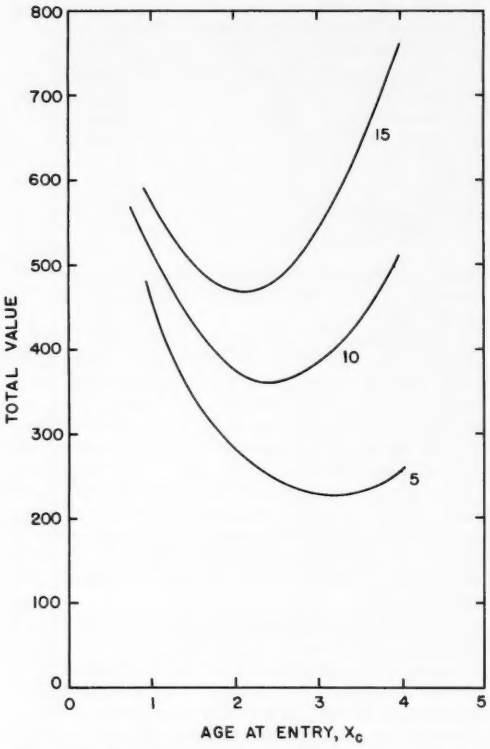

FIG. 2. Total value of fishery with conventional size limits as a function of age at entry with three different values (5, 10, and 15) for trophy fish with a conventional size limit.

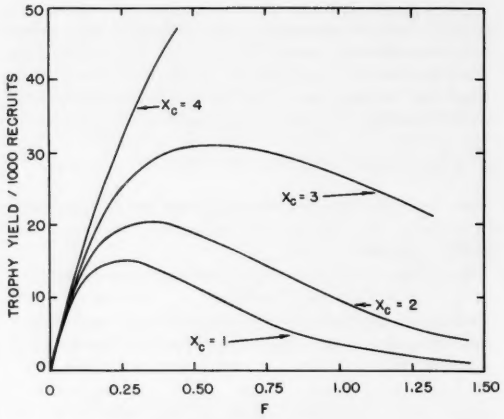

FIG. 3. Trophy catch per 1000 recruits with a conventional size limit as a function of fishing mortality with different ages of entry into the exploited stock, x_c, and a conventional size limit.

then begins to slowly decrease (Fig. 3). The level of the maximum and the value of F at which the maximum occurs are determined by x_c. Changing F has a substantial impact on trophy catch with $x_c = 1.0$ (Fig. 3); the optimum value of F is 0.25 when $x_c = 1.0$. Most trout fisheries might be considered overfished in terms of the production of trophy fish, but decreasing F to produce the maximum number of trophy fish drastically reduces the total catch. For example, if $x_c = 1.0$, $R = 1000$, and F is reduced from 0.50 to 0.25 to optimize trophy catch, total catch decreases from 417 to 263 and trophy catch increases from 11 to only 15. In summary, trophy catch can be increased by decreasing F or by increasing x_c but both result in a large decrease in total catch.

The prediction of the model that increasing x_c will drastically decrease total catch was verified in an experiment reported by Hunt et al. (1962). In their experiment three different sets of regulations were applied to the Lawrence Creek brook trout fishery: (1) 15.24-cm size limit with a bag of 10, (2) 22.86-cm size limit with a bag of 5, and (3) no size or bag limit. The catch with no limits was the same as the catch with a 15.24-cm limit and a bag of 10 because anglers would not keep smaller trout and few were able to catch the bag limit of 10 fish. The higher size limit of 22.86 cm dramatically reduced the total catch as well as the number of angler trips. Growth declined because of increased competition for food, and natural mortality increased. Trophy catch did not increase measurably with the higher size limit. The few years of data available and the high variability from year to year in catch of fish larger than 22.86 cm do not enable detection of an increase in trophy catch of the small size predicted by the model. The observed increase in natural mortality and decrease in growth resulting from the higher size limit could have offset the small increase in trophy catch predicted by the model.

Application of the model indicates that slot limits increase trophy catch a small amount without severly reducing total

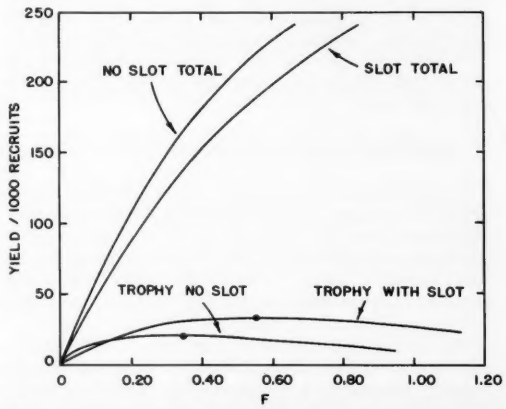

FIG. 4. Total yield and trophy yield as a function of fishing mortality with a conventional size limit and a slot limit with $x_c = 2.0$, $x_f = 3.0$, and $x_{tr} = 4.0$.

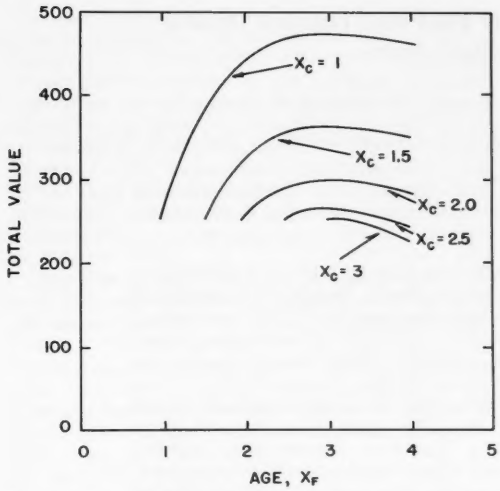

FIG. 5. Total value of a fishery with a slot limit with $x_{tr} = 4$ as a function of x_f with different ages at entry, x_c.

catch. For example, consider a slot limit with $R = 1000$, $x_f = 3$, $x_{tr} = 4$, and $F = 0.50$. With an age of entry of $x_c = 1$ the total yield without the slot limit is 417 and 11 trophy fish are caught. With the slot limit 398 fish are caught and the number of trophy fish is 19. A 5% decrease in total catch produces nearly a 50% increase in trophy catch. With no slot limit and $x_c = 2$, total catch is 207 and the trophy catch is 19. With the slot limit trophy catch increases to 31 (63% increase) and total catch decreases to only 176 (15% decrease). The slot limit flattens the curve of trophy catch vs. F and increases the optimum F from 0.35 to 0.56 (Fig. 4).

When slot limits are applied trophy catch can be increased by changing both x_c and x_f, but as trophy catch increases total catch decreases. If values are assigned to non-trophy and trophy fish, the values of x_c and x_f that give a maximum value for the fishery can be calculated. For example, let $R = 1000$, $F = 0.50$, $V_{tr} = 5$, and $V_{nt} = 1$; then the value of the fishery is a maximum with $x_c = 1.0$ and $x_f = 2.95$. The changes in value with changes in x_c and x_f are shown in Fig. 5. Increasing x_c from age 1 to age 2 decreases the total value substantially but further increases in x_c do not produce large decreases in value. Increasing x_f from 1 to 2.95 produces at first a large and then a progressively smaller increase in total value. Total value decreases slowly as x_f increases beyond the optimum at 2.95. A fishery without a slot limit is obtained when $x_f = 4$, and it is clear that the optimum slot limit with $x_f = 2.95$ increases total value of the fishery by only a small amount (Fig. 5).

The above analysis indicates that slot limits will produce small increases in trophy catch without causing a large decrease in total catch. The highest value for the fishery is obtained by setting x_c as small as is acceptable to fishermen and then setting x_f at the age where the maximum total value occurs.

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Many of may ideas concerning slot limits developed after discussions with R. Clark of the Michigan DNR and several members of the Ann Arbor Chapter of Trout Unlimited. Clark suggested separation of total catch into a non-trophy catch and a trophy catch.

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Complementarity in the Use of Food and Thermal Habitat by Lake Michigan Fishes

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CROWDER, L. B., J. J. MAGNUSON, AND S. B. BRANDT. 1981. Complementarity in the use of food and thermal habitat by Lake Michigan fishes. Can. J. Fish. Aquat. Sci. 38: 662–668.

The potential for ecological segregation of Lake Michigan fishes was examined by comparing diets and thermal habitat use of common species. Samples were collected by bottom trawling ($N = 68$) off Grand Haven, Michigan, September 7–13, 1977. Five common species exhibited complementarity in the use of food and thermal habitat resources. During the day, adult alewife (*Alosa pseudoharengus*), and rainbow smelt (*Osmerus mordax*) had similar diets but occupied somewhat different thermal habitats. Young-of-the-year (YOY) alewives segregated from adult alewife and rainbow smelt on both habitat and food. Spottail shiner (*Notropis hudsonius*), YOY alewives, and yellow perch (*Perca flavescens*) used similar thermal habitats but fed on different prey. Trout-perch (*Percopsis osmiscomaycus*) tended to segregate from the others based on both food and thermal habitat but may experience diffuse competition. Adults of the three native species consume entirely different prey than exotic alewife and rainbow smelt. The native species which declined during the invasion of alewife and rainbow smelt were those with apparently similar habitat and food requirements to the exotics. These data suggest that competition is important in maintaining the structure of the Lake Michigan fish community.

Key words: competition, fishes, food, habitat, Lake Michigan, predation, temperature

CROWDER, L. B., J. J. MAGNUSON, AND S. B. BRANDT. 1981. Complementarity in the use of food and thermal habitat by Lake Michigan fishes. Can. J. Fish. Aquat. Sci. 38: 662–668.

En comparant le régime alimentaire et l'utilisation de l'habitat thermique d'espèces communes, nous avons étudié le potentiel d'une ségrégation écologique des poissons du lac Michigan. Des échantillons ont été recueillis par chalutages sur le fond ($N = 68$) au large de Grand Haven (Michigan) du 7 au 13 septembre 1977. Cinq espèces communes montrent une complémentarité dans leur utilisation des ressources alimentaires et de l'habitat thermique. Le jour, les gaspareaux adultes (*Alosa pseudoharengus*), les et les éperlans arc-en-ciel (*Osmerus mordax*) ont des régimes alimentaires semblables, mais occupent toutefois des habitats thermiques différents. Les jeunes gaspareaux de l'année se distinguent des gaspareaux adultes et des éperlans arc-en-ciel autant du point de vue de l'habitat que du point de vue de la nourriture. Les queues à tache noire (*Notropis hudsonius*), les gaspareaux et les perchaudes (*Perca flavescens*) de l'année utilisent les mêmes habitats thermiques, mais se nourrissent de proies différentes. Les omiscos (*Percopsis omiscomaycus*) tendent à différer des autres espèces tant sous le rapport de la nourriture que de l'habitat thermique, mais peuvent subir une concurrence diffuse. Les adultes des trois espèces indigènes se nourrissent de proies complètement différentes de celles du gaspareau et de l'éperlan arc-en-ciel. Les espèces indigènes qui déclinèrent au moment de l'invasion du gaspareau et de l'éperlan arc-en-ciel sont celles dont l'habitat et le régime alimentaire étaient apparemment semblables à ceux des espèces exotiques. D'après ces données, la concurrence jouerait un rôle important dans le maintien de la structure de la communauté ichtyologique du lac Michigan.

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THE Lake Michigan fish community has been subjected to a series of perturbations for the past 50 years (Wells and McLain 1973; Christie 1974), which have led to many changes including habitat use, prey resources, and species composition. The most notable changes followed the invasion of rainbow smelt in the 1920s (Wells and McLain 1973) and sea lamprey (*Petromyzon marinus*) first reported in 1936 (Applegate 1950). The sea lamprey virtually decimated stocks of the larger piscivores, notably lake trout (*Salvelinus namaycush*), which ultimately opened the way for the proliferation of the two exotic planktivores, alewife and rainbow smelt (Smith 1970).

During the period of smelt and alewife increase, many native fish species declined in abundance and several probably became locally extinct in Lake Michigan (Wells and McLain 1973). Emerald shiner (*Notropis atherinoides*), lake herring (*Coregonus artedii*), and five species of deepwater cisco (*Coregonus* spp.) are no longer common in the lake. Numerous hypotheses have been suggested to account for these declines, particularly competition for food between alewife, smelt, and native species (Smith 1970; Wells and McLain 1973). Predation by smelt and alewife on early life history stages of native species may also have been important (Wells and McLain 1973; Crowder 1980).

If competition has been an important force structuring the Lake Michigan fish community, we would expect to observe complementarity (Schoener 1974) in the use of food and habitat resources among existing species. If two competitors have similar diets, we may expect habitat partitioning; if similar habitats are used, we may expect differences in diets. We have provided evidence for thermal habitat partitioning in Lake Michigan fishes (Brandt et al. 1980). Distributions of each of the six most abundant species (alewife, rainbow smelt, spottail shiner, trout-perch, deepwater sculpin (*Myoxocephalus quadricornis*), and yellow perch) were significantly associated with particular temperatures. This partitioning of thermal habitat often differed between species or size-classes within a species. A general broadening of thermal habitat distributions occurred at night when major species vertically migrate (Brandt et al. 1980; Janssen and Brandt 1980). The purpose of this paper is to contrast the use of food resources among the five common species with their use of thermal habitat and to determine whether the patterns observed are consistent with a hypothesis of complementary resource use.

Methods

Fishes in the zone of intersection between the thermocline and lake bottom were sampled off Grand Haven, Michigan, September 7–13, 1977. Fishes were collected day ($N = 28$) and night ($N = 40$) during 15-min tows with a semiballoon otter trawl. The trawl had a 7.6-m headrope and a body of 2 cm stretch mesh nylon; the cod end was lined with 0.6 cm stretch mesh. A thermistor attached to the trawl's headrope allowed us to categorize the 68 hauls into nine thermal strata each of 2°C. Full details of the sampling design are in Brandt et al. (1980) as are the thermal distributions of each species.

Up to 50 individuals per species per trawl haul were frozen using dry ice and subsequently measured and subsampled for stomach analyses. A total of 1161 stomachs from five common species was examined. For alewife, 6.8% of the stomach volume was subsampled to enumerate prey. For all other species, total stomach contents were enumerated. Crustaceans were identified to species when possible, but broader taxonomic categories are used here since many prey could not be specifically identified because of digestion.

Samples were sufficient to characterize day and night diets of alewife, rainbow smelt, spottail shiner, trout-perch, and yellow perch. Diets are characterized as proportion by numbers in various prey classes pooled from all individuals examined. Numerically rare prey which occurred in many of the stomachs are described by percentage of frequency of occurrence. Data from Brandt et al. (1980) were used to calculate proportional catch per unit effort in thermal habitat used by the five common species considered above in respect to diet (cf. Fig.3 in Brandt et al. 1980). We have detected an error in our calculation of the catch per unit effort during day for adult rainbow smelt (cf. Brandt et al. 1980). Rainbow smelt are widely distributed between 7 and 18°C but do not reach maximum abundance at 7–8°C. There are no significant peaks of abundance within this zone. All thermal habitat data used here include the corrected catch per unit effort calculations for smelt. Our interpretations will concentrate on use of food and thermal habitat during the day (05:30–19:30) since alewife and possibly rainbow smelt vertically migrate off the bottom at night (Janssen and Brandt 1980) and may provide misleading conclusions.

Proportional similarity, C_{xy}, in the use of food taxa and thermal habitats was calculated as follows (Schoener 1970; cf. Hurlbert 1978).

$$C_{xy} = \sum_i \min (P_{xi}, P_{yi})$$

where P_{xi} is the proportional contribution of resource i to the total resource use by species x, P_{yi} is the proportional contribution of resource i to the total resource use by species y.

Results

Similarity in Diets of Common Fishes

We examined the similarity in diets between each species pair to assess potential competitive interactions for food. Diets are detailed separately for day and for night in Tables 1 and 2 for YOY alewife, adult alewife, rainbow smelt, spottail shiner, trout-perch, and yellow perch. These numbers are used to calculate the proportional similarity in the diets between each species pair with YOY and adult alewife being treated for computations as different species since their habitats differed significantly (Brandt et al. 1980).

Differences and similarities among species are apparent. Adult alewife, YOY alewife, and smelt concentrate on *Daphnia* and copepods both day and night. Spottail shiner eat large numbers of *Eurycercus* and chydorid cladocera during day and night but also include significant numbers of insects during day and fish eggs at night. Trout-perch contained large numbers of insects during day and both insects and *Pontoporeia* at night. Yellow perch contained large numbers of *Pontoporeia* during day and *Eurycercus* at night. In

TABLE 1. Day stomach contents (05:30–19:30) of common fishes in Lake Michigan caught in bottom trawls off Grand Haven, Michigan, in September 1977. Measured as frequency of occurrence (% of fish) and proportion (*P*) by numbers in the diet.

	YOY Alewife		Adult Alewife		Rainbow smelt		Spottail shiner		Trout-perch		Yellow perch	
Prey	%	P	%	P	%	P	%	P	%	P	%	P
Cladocera												
Leptodoridae	15	<0.01	30	<0.01	9	<0.01	0	0	0	0	0	0
Bosminidae	53	0.02	40	<0.01	8	<0.01	0	0	0	0	0	0
Daphnidae	95	0.26	96	0.93	60	0.95	6	<0.01	1	<0.01	0	0
Eurycercinae	15	0.02	1	<0.01	3	<0.01	6	0.55	7	<0.01	22	0.10
Chydoridae	15	<0.01	27	<0.01	7	<0.01	20	<0.01	0	0	0	0
Copepoda												
Calanoida	97	0.35	96	0.04	33	0.02	0	0	1	<0.01	0	0
Cyclopoida	100.0	0.33	89	0.02	10	<0.01	6	<0.01	1	<0.01	11	<0.01
Mysidacea												
Mysis relicta	0	0	5	<0.01	3	0.03	0	0	0	0	0	0
Amphipoda												
Pontoporeia affinis	3	<0.01	21	<0.01	8	0.01	11	<0.01	42	0.15	50	0.75
Insecta												
Chironomidae	15	<0.01	10	<0.01	12	<0.01	83	0.38	88	0.84	72	0.14
Unident. insect	0	0	0	0	0	0	15	0.06	0	0	0	0
Fish												
Larvae	0	0	0	0	31	<0.01	2	<0.01	1	<0.01	11	<0.01
Eggs	0	0	0	0	0	0	2	<0.01	0	0	0	0
Other	0	0	1	<0.01	1	<0.01	1	<0.01	0	0	0	0
Number of stomachs	60		101		128		81		78		21	
% empty	0		0		29		43		11		14	
Fish size $\bar{X}$ (SD) (mm SL)	55(10)		133(9)		104(19)		78(24)		77(15)		89(35)	

TABLE 2. Night stomach contents (19:30–05:30) of common fishes in Lake Michigan caught in bottom trawls off Grand Haven, Michigan, in September 1977. Measured as frequency of occurrence (% of fish) and proportion (*P*) by numbers in the diet.

	YOY Alewife		Adult Alewife		Rainbow smelt		Spottail shiner		Trout-perch		Yellow perch	
Prey	%	P	%	P	%	P	%	P	%	P	%	P
Cladocera												
Leptodoridae	10	<0.01	10	<0.01	0	0	0	0	0	0	0	0
Bosminidae	67	0.06	25	<0.01	4	<0.01	0	0	0	0	0	0
Daphnidae	88	0.24	100	0.30	23	0.76	1	<0.01	<1	<0.01	10	<0.01
Eurycercinae	2	<0.01	5	<0.01	7	<0.01	56	0.39	7	0.01	58	0.77
Chydoridae	9	<0.01	25	<0.01	5	<0.01	28	<0.01	2	<0.01	6	<0.01
Copepoda												
Calanoida	77	0.50	85	0.62	8	0.05	0	0	0	0	0	0
Cyclopoida	84	0.20	85	0.07	8	0.02	1	<0.01	<1	<0.01	4	<0.01
Mysidacea												
Mysis relicta	0	0	30	<0.01	43	0.10	1	<0.01	2	<0.01	0	0
Amphipoda												
Pontoporeia affinis	0	0	30	<0.01	10	<0.01	19	0.16	76	0.55	30	0.12
Insecta												
Chironomidae	4	<0.01	5	<0.01	13	0.07	33	0.14	87	0.43	52	0.10
Unident. insect	0	0	0	0	0	0	19	<0.01	0	0	0	0
Fish												
Larvae	0	0	0	0	31	<0.01	1	<0.01	<1	<0.01	0	0
Eggs	0	0	0	0	0	0	10	0.29	0	0	0	0
Other	4.5	<0.01	5	<0.01	2	<0.01	1	<0.01	<1	<0.01	2	<0.01
Number of stomachs	57		20		193		133		218		71	
% empty	0		0		40		48		10		30	
Fish size $\bar{X}$ (SD) (mm SL)	45(11)		128(28)		101(21)		83(15)		81(18)		56(23)	

TABLE 3. Proportion of each fish species caught in 2°C temperature strata relative to total catch of each species in Lake Michigan during day (D) 05:30–19:30 and night (N) 19:30–05:30) in September 1977.

Temperature strata (°C)	YOY Alewife		Adult Alewife		Rainbow smelt		Spottail shiner		Trout-perch		Yellow perch	
	D	N	D	N	D	N	D	N	D	N	D	N
3–4	0	0	0	0	0	0	0	0	0	0	0	0
5–6	0	0.04	0	0.20	0	0.03	0	0	0.03	0.08	0	0
7–8	0	0.03	0.04	0.12	0.15	0.04	0	0.03	0.05	0.42	0	0.27
9–10	0	0.04	0.08	0.02	0.19	0.03	0	0	0.05	0.02	0.02	0.03
11–12	0	0.03	0.29	0.09	0.10	0.44	0	0.10	0.02	0.12	0	0.06
13–14	0	0.08	0.37	0.31	0.23	0.32	0	0.09	0	0.14	0	0.09
15–16	0	0.09	0.15	0.22	0.28	0.10	0.16	0.13	0.49	0.10	0.33	0.16
17–18	0.03	0.68	0	0.04	0.05	0.05	0.07	0.65	0.24	0.11	0.07	0.40
19–20	0.97	[a]	0.07	[a]	0	[a]	0.78	[a]	0.12	[a]	0.58	[a]

[a]No data.

summary, the prey of YOY alewife, adult alewife, and rainbow smelt are similar; the diets of spottail shiner, trout-perch, and yellow perch appear to be different from each other and exclusive from alewife and smelt.

The overall similarities in daytime diet when calculated from the proportions of prey taxa in Tables 1 and 2 ranged from $C = 0$ to $C = 0.95$. Adult alewife and rainbow smelt have the most similar diets, exotic and native species pairs have almost no overlap in diet, and similarity between all paired combinations of yellow perch, spottail shiner, and trout-perch range from $C = 0.24$ to $C = 0.38$. The YOY alewife has a $C = 0.32$ similarity with adult alewife and a $C = 0.28$ with rainbow smelt.

SIMILARITY IN THERMAL HABITATS

The seasonal depth distribution of Lake Michigan fishes was first outlined by Wells (1968). Though valuable insights were provided on seasonal changes in depth distributions, the coarse scale of trawl samples with depth and lack of replication led us to detail the distribution of these fishes on a finer scale. We found that in the metalimnion fish are segregated with respect to temperature as evidenced by their association with fixed temperature zones even though the position of the thermocline was highly dynamic (Brandt et al. 1980).

Similarities in daytime thermal habitat use (based on proportions in Table 3) ranged from $C = 0.03$ to $C = 0.87$. No pair had zero overlap in habitat use. The pairs with the highest habitat similarity were spottail shiner–yellow perch and YOY alewife–spottail shiner both with $C = 0.81$. YOY alewife had low habitat overlaps with rainbow smelt $C = 0.03$ and with adult alewife $C = 0.08$. All other pairs had intermediate overlap with $C = 0.15 - 0.61$.

Discussion

COMPLEMENTARITY IN FOOD AND HABITAT USE

Similarity between competing species in the use of one resource often implies dissimilarity in the use of another resource. For example, if two competitors use similar foods, we might expect habitat partitioning; if similar habitats are used, we expect differences in fish diets. The daytime diet and habitat use data presented above clearly indicated that some of the species pairs had similar diets and others occupied similar habitats. Is complementarity in respect to the two resources occurring? The answer appears to be yes (Fig. 1).

When we compare all species pairs during the day, adult alewife and rainbow smelt consumed very similar foods but tended to segregate based on thermal habitat (Fig. 1). Adult alewife and rainbow smelt are clearly segregated from YOY alewife based on thermal habitat; food use was more similar than habitat use. YOY alewife, spottail shiner, and yellow perch occupy similar thermal habitats and clearly segregate by food taxon during the day (Fig. 1). Spottail shiner, trout-perch, and yellow perch differ profoundly in food habitats from alewife and rainbow smelt; no significant food overlaps exist between exotic and native species. Trout-perch have moderate overlaps in diet and habitat with both spottail and yellow perch and may experience diffuse competition (MacArthur 1972) from both species.

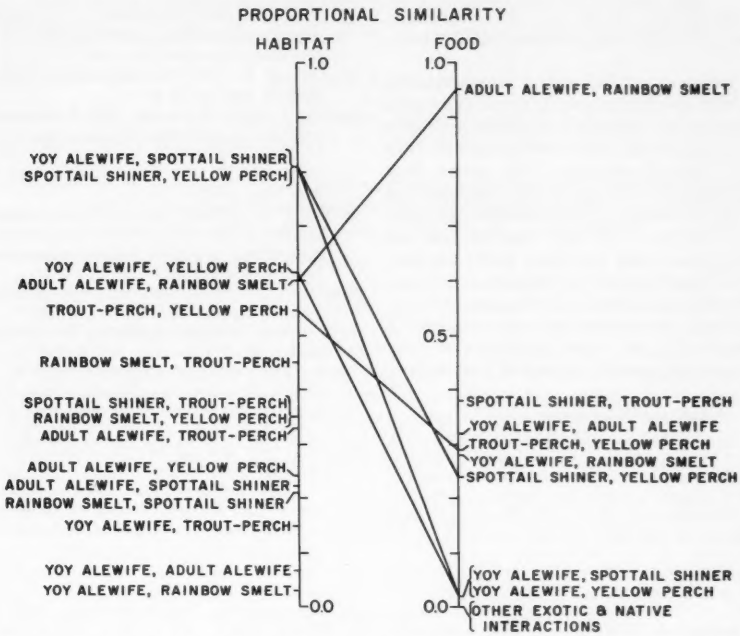

FIG. 1. Daytime proportional similarity in food and thermal habitat use by Lake Michigan fishes taken in bottom trawls off Grand Haven in September 1977.

Native species analyzed here tend to segregate based on food taxon or have moderate overlaps in both food and habitat. Exotic species tend to segregate by habitat. It is not surprising that food segregation may be more common in a co-evolved group since trophic morphology and feeding behaviors tend to be less flexible than habitat choice.

COMPETITION AND THE FATE OF NATIVE FISHES

Resource partitioning data are insufficient to prove competition has been an important factor in the Lake Michigan fish community (Sale 1979). Indeed, the history of repeated establishment of exotics to this community suggests that it is likely to be far from any sort of competitive equilibrium. However, we also know that in controlled field experiments, when fish are subject to intense competition, shifts in resource use can be rapid (Werner and Hall 1976, 1977, 1979). If the decline of several native fishes (Wells and McLain 1973) and the depression of the zooplankton resource base during the alewife increase (Wells 1970) can be attributed to competition for food (cf. Crowder 1980), then we can be assured that competition can act rapidly to alter large-scale system characters in Lake Michigan. Since selection of habitat and food resources is somewhat behavioral we might expect resource partitioning to be elastic and very responsive to competition.

None of the three common native species (and size-classes) examined here have significant diet overlaps with either alewife or rainbow smelt. The species which declined most drastically during the increase of alewives and smelt were those with similar feeding habits. Emerald shiners (*Notropis atherinoides*), young lake herring (*Coregonus artedii*), and young deepwater ciscoes (*Coregonus* sp.) fed almost exclusively on microzooplankton (Wells and Beeton 1963; Flittner 1964; Scott and Crossman 1973; Wells and McLain 1973). Emerald shiners were formerly common nearshore (Wells and McLain 1973) and young coregonines were known to occupy mid-depths (Wells 1968) which may have allowed overlaps with alewife and rainbow smelt. Yellow perch also declined somewhat during the alewife increase (Wells 1977), perhaps because of competition for food between young perch and alewife or to predation by alewife on perch larvae (Wells 1977; Crowder 1980). Trout-perch and spottail shiners were relatively unaffected by the alewife increase — their diets do not overlap. It is possible that the native species which survived the invasion of alewife and smelt were those which differed significantly in food use or were able to undergo diet or habitat shifts that minimized negative effects.

Interpretations from these data must be considered in light of the assumptions and limitations of the study. We have assumed that thermal habitat distributions for these fishes during day can be sufficiently assessed by bottom trawling (cf. Brandt et al. 1980). Food habits of fishes at different temperatures may reflect differences in prey availability in addition to prey selection; no direct estimates of prey availability were made. Since few juvenile fishes were caught in our trawls, we cannot comment on potential interactions involving larval or juvenile fishes. Finally, the patterns of resource use we observed during this survey should not be extrapolated

uncritically to other seasons of the year. Our observations may reflect summer, postspawning, resource subdivision in these fishes.

The apparent partitioning of food and habitat resources by the current Lake Michigan fish community should allow them to reduce competition. The historical data suggest that native species with food habits similar to alewife and smelt declined most dramatically during the invasion of the exotics. Both historical and contemporary data suggest that competition has been important in structuring the Lake Michigan fish community. But predation by alewife and smelt on eggs and larvae of native species may also have been important (Crowder 1980). To assess further the importance of competition among Lake Michigan fishes we need detailed information on the use of food resources relative to prey availability, laboratory studies on food and habitat preferences of these species, and a more experimental approach to field studies.

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Biochemical Genetic Analysis of Population Differentiation in Greenland Halibut (*Reinhardtius hippoglossoides*) from the Northwest Atlantic, Gulf of St. Lawrence, and Bering Sea

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FAIRBAIRN, D. J. 1981. Biochemical genetic analysis of population differentiation in Greenland halibut (*Reinhardtius hippoglossoides*) from the Northwest Atlantic, Gulf of St. Lawrence, and Bering Sea. Can. J. Fish. Aquat. Sci. 38: 669–677.

Greenland halibut (*Reinhardtius hippoglossoides*) from the Northwest Atlantic Ocean, the Gulf of St. Lawrence, and the Bering Sea were analyzed for allele and genotype frequencies at 16 electrophoretically detectable protein loci. Thirteen of these loci were monomorphic, with identical mobilities in all samples. One locus (MDH-1) was polymorphic only in the Bering Sea sample. Two loci, PGM and PHI-2, were polymorphic in all samples. An analysis of allele frequencies at these latter loci indicated that Greenland halibut from the Northwest Atlantic area form a single genetically homogeneous stock, but that those in the Gulf of St. Lawrence form a separate though not completely isolated stock. Greenland halibut from the Bering Sea differ greatly from these, and a genetic distance estimate based on all 16 loci suggested genetic divergence at the subspecific level between the two oceans.

Key words: Greenland halibut, *Reinhardtius hippoglossoides*; biochemical genetic variation, electrophoresis, phosphoglucomutase, phosphohexose isomerase, genetic distance

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L'auteur a examiné des flétans du Groenland (*Reinhardtius hippoglossoides*) en provenance de l'Atlantique nord-ouest, du golfe du Saint-Laurent et de la mer de Béring, afin de déterminer la fréquence d'allèles et de génotypes à 16 loci de protéines détectables par électrophorèse. Treize de ces loci sont monomorphes, doués d'une mobilité identique, dans tous les échantillons. Un locus (MDH-1) n'est polymorphe que dans l'échantillon de la mer de Béring. Deux loci (PGM et PHI-2) sont polymorphes dans tous les échantillons. Une analyse de la fréquence d'allèles à ces derniers loci indique que les flétans du Groenland de l'Atlantique nord-ouest forment un stock unique génétiquement homogène et que ceux du golfe du Saint-Laurent sont un stock séparé mais non complètement isolé. Les flétans du Groenland de la mer de Béring diffèrent beaucoup de ceux-ci, et une estimation des distances génétiques sur les 16 loci suggère qu'il y a divergence génétique au niveau sous-spécifique entre les deux océans.

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THE Greenland halibut (*Reinhardtius hippoglossoides*) is a flatfish of the family Pleuronectidae. Several aspects of its distribution and life history suggest that this flatfish may be unusually mobile in both the adult and larval stages. In the Northwest Atlantic, spawning is thought to occur mainly in the deep water of the Davis Strait, south of 66°45′N (Jensen 1935; Smidt 1969; Templeman 1973; Chumakov et al. 1978). Eggs and larvae then drift northward with the West Greenland current toward Greenland and Baffin Island. Those captured by the Labrador current drift south to colonize the continental slopes of Labrador and Newfoundland, extending as far south as Georges Bank (Templeman 1973). Such long-distance drift and migration is facilitated by the unusually long larval period in this species: larvae remain bilaterally symmetrical up to 57 mm in length, and are pelagic up to 70 mm in length (Hubbs and Wilimovsky 1964). Mature, adult Greenland halibut are thought to migrate from the slopes and banks back to deeper water to spawn (Jensen 1935; Smidt 1969; Pitt 1974; Bowering 1978). This pattern of spawning and migration suggests that most of the Greenland halibut in the Northwest Atlantic form one continuous stock (Pitt 1974; Pinhorn 1976; Zilanov et al. 1976). There is some evidence, however, for

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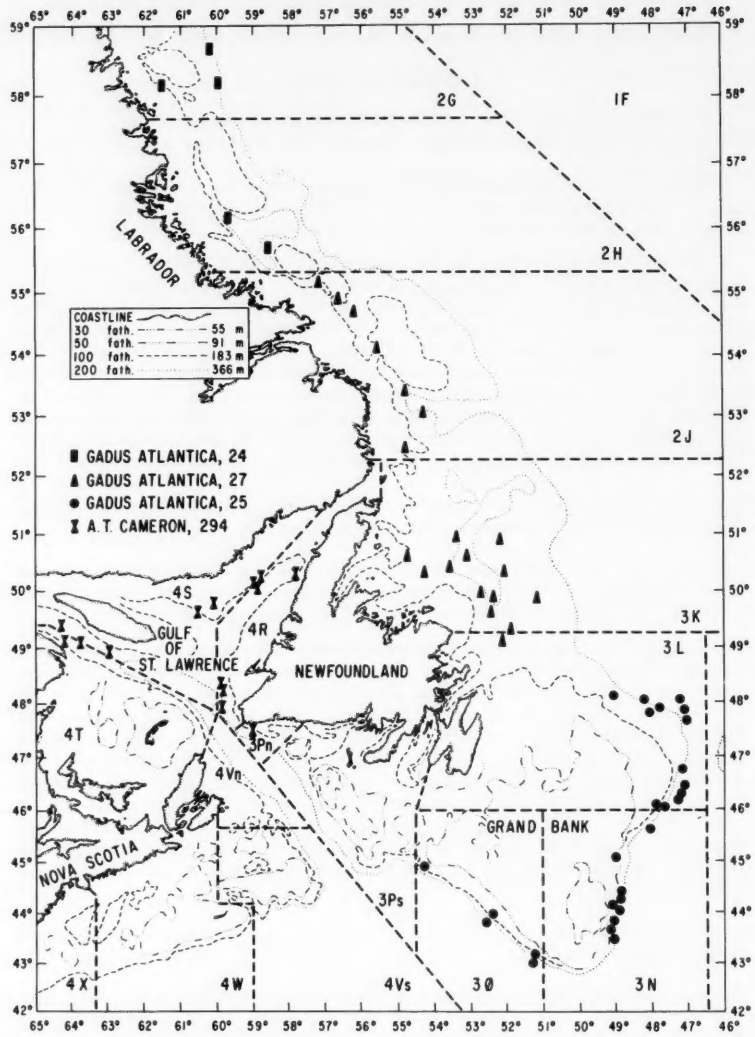

FIG. 1. Distribution of Greenland halibut samples by trip in the Gulf of St. Lawrence and Northwest Atlantic. Broken lines delineate the Northwest Atlantic Fisheries Organization (NAFO) subareas. Henceforth, the Gadus Atlantica trips 24, 25, and 27 will be designated Northwest Atlantic samples 1, 2, and 3, respectively. Similarly, the sample gathered by the A. T. Cameron will be referred to as the Gulf of St. Lawrence sample.

separate stocks within the Gulf of St. Lawrence (Lear 1970; Templeman 1970) and around Iceland (Paschen 1968). Greenland halibut are also found in Ungava Bay, the eastern North Atlantic, the Barents Sea, the Bering Sea, and the North Pacific (Fedorov 1971; Hubbs and Wilimovsky 1964; Templeman 1973). Those in the Atlantic and Pacific oceans closely resemble each other (Hubbs and Wilimovsky 1964) and are considered a single species. Atlantic Greenland halibut, however, have been found to differ significantly from those from the Pacific in both meristic (Templeman 1970) and morphometric characters (Vernidub and Panin 1937, from Hubbs and Wilimovsky 1964). This suggests the possibility of genetic differentiation at least at the stock level, between the two oceans.

To test the above hypotheses of population structure in the Greenland halibut, I examined the distribution of electro-

phoretically detectable protein variants in the Northwest Atlantic, the Gulf of St. Lawrence, and the Bering Sea. The a priori hypotheses predicted little differentiation along the banks and slopes of Labrador and Newfoundland. The Gulf of St. Lawrence, thought to have its own breeding population, might be expected to differ from this Northwest Atlantic stock, while the Bering Sea Greenland halibut should differ still more. These were the simplest genetic hypotheses that could be generated from the proposed population structure and so provided a logical starting point for this study.

Although 16 electrophoretically detectable protein loci were assayed in Greenland halibut, only 2 were found to be polymorphic and suitable for the analysis of population structure. Much of the following analyses thus concern only these two loci; phosphoglucomutase (E. C. 2.7.5.1) (PGM) and glucosephosphate isomerase (phosphohexose isomerase, E. C. 5.3.1.9) (PHI). Malate dehydrogenase (E. C. 1.1.1.38) (MDH) was polymorphic only in the Bering Sea sample and was useful only in the comparisons of this sample with the Atlantic samples.

Methods

Sample Collection

The distribution of Greenland halibut samples in the Northwest Atlantic and Gulf of St. Lawrence can be seen in Fig. 1. All of these samples were collected during routine survey cruises by personnel of the Groundfish Program, Fisheries and Oceans Canada, Northwest Atlantic Fisheries Center, St. John's, Newfoundland. The Gulf samples were collected via $^1/_2$-h tows using a standard 41-5 lined otter trawl. The remaining samples were collected via $^1/_2$-h tows using an Engels high-rise, lined, otter trawl. The Bering Sea samples (Fig. 2) were collected by personnel of the U.S. National Marine Fisheries Service, Seattle, Washington.

The Pacific samples consisted of either whole fish or the anterior one-third of the fish, containing the heart and liver. The Atlantic samples consisted of ~ 1 cm^2 each of white muscle and liver, plus the whole heart. These tissues were frozen separately in plastic bags and stored at -20°C until processed.

Biochemical Techniques

Samples were prepared for electrophoresis simply by mechanical disruption in an equal volume of 0.9% saline. (More complex methods of preparation such as homogenization, sonication, centrifugation, and the addition of various stabilizing agents such as EDTA and mercaptoethanol were tried but did not noticeably alter the results.) Small filter paper wicks were inserted into the tissue suspension, blotted on paper towelling, and inserted into a slit at the gel origin. The gels measured 280 × 145 × 5 mm and were cooled with ice packs during the electrophoretic run. All routine runs for PGM and PHI were made using 12.5% potato starch (Connaught lot No. 350-1) and Poulik's discontinuous Tris–citrate buffer system (Selander et al. 1971). MDH was best visualized with a continuous bis-Tris buffer (electrode buffer: 8.41 g citric acid, 52.97 g bisTris/L; gel buffer: 50 ml electrode buffer/L) (H. Tsuyuki personal communication).

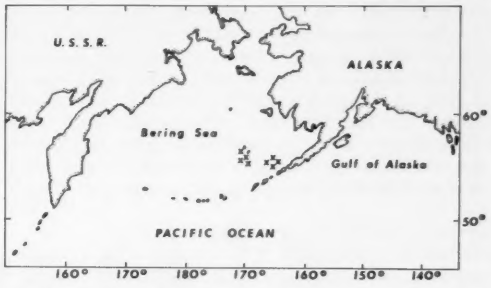

FIG. 2. Distribution of Greenland halibut samples from the Bering Sea.

Phosphoglucomutase was visualized by incubation at 37°C for 15 min in a staining solution composed of 15 ml 0.2 mol/L Tris (pH 8.0), 75 mL water, 15 mL 0.1 mol/L magnesium chloride, 60 units of glucose-6-phosphate dehydrogenase, 15 mg NADP, 15 mg MTT, 15 mL 0.05 mol/L glucose-1-phosphate, and 6 mg phenazine methosulfate (PMS) (from Selander et al. 1971). Phosphohexose isomerase was visualized via incubation at 37°C for $^1/_2$ h in a staining solution composed of 8 mg fructose-6-phosphate, 11 mg NADP, 11 mg MTT, 4 mg PMS, 80 units glucose-6-phosphate dehydrogenase, 5 mL 0.1 mol/L magnesium chloride, 25 mL 0.05 mol/L Tris (pH 8.0), and 75 mL water (modified from Brewer 1970). MDH was visualized by incubation at 37°C for $^1/_2$ h in the following staining solution: 20 mL 0.2 mol/L Tris (pH 8.0), 10 mL 1.0 M malate, 20 mg NAD, 5 mg PMS, and 20 mg MTT (Selander et al. 1971).

Results

Only one area of activity was found for PGM. Activity was greatest in muscle and least in liver, but all three tissues showed the same patterns of variability (Fig. 3). Repeated freezing and thawing of samples resulted in the formation of secondary anodal PGM isozymes (Fisher and Harris 1972; Dawson and Greene 1975; Harris 1975; Beckman 1978), but these could be easily distinguished from the isozymes produced by allelic variation. These patterns suggest a monomer with a single locus and several alleles. This corresponds to observations of PGM in other fish species (Utter and Hodgins 1970; Utter et al. 1973; Altukhov et al. 1975), although both multiple loci and multiple-banded homozygotes have been reported for some species (Place and Powers 1978; Kimura 1978; Smith and Jamieson 1978; Odense et al. 1978). Six PGM alleles were found, and their mobility was scored relative to the mobility of the common allele, as suggested by Allendorf and Utter (1979).

Phosphohexose isomerase showed two distinct areas of activity corresponding to two loci (Fig. 4). The most anodal locus (PHI-2) was monomorphic and appeared in all three tissues. The second locus (PHI-1) ran cathodally to PHI-2 and was polymorphic with seven alleles. PHI-1 was the most active locus in muscle, was less active than PHI-2 in heart, and did not appear at all in liver. Repeated freezing and thawing resulted in the formation of faint secondary isozyme bands at the PHI-1 locus, but these were easily distinguished

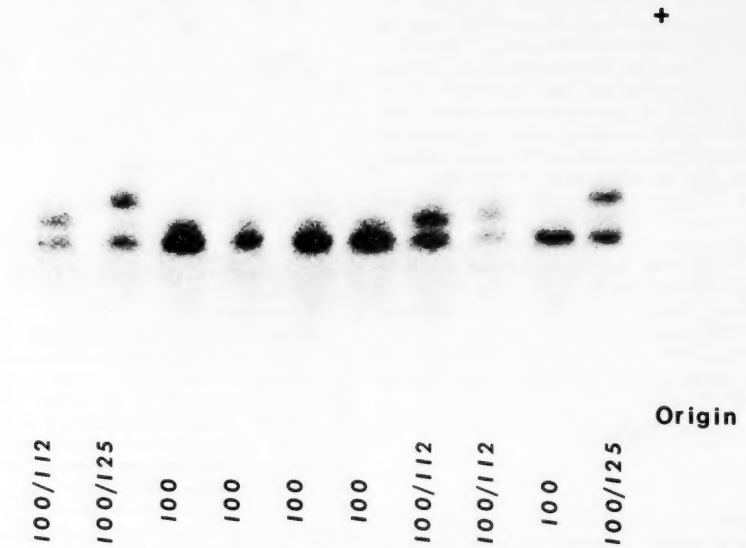

FIG. 3. Representative phosphoglucomutase phenotypes from white muscle. Faint, secondary, anodal bands induced by repeated freezing and thawing of samples can be seen, particularly in the third, fifth, and sixth samples from the left.

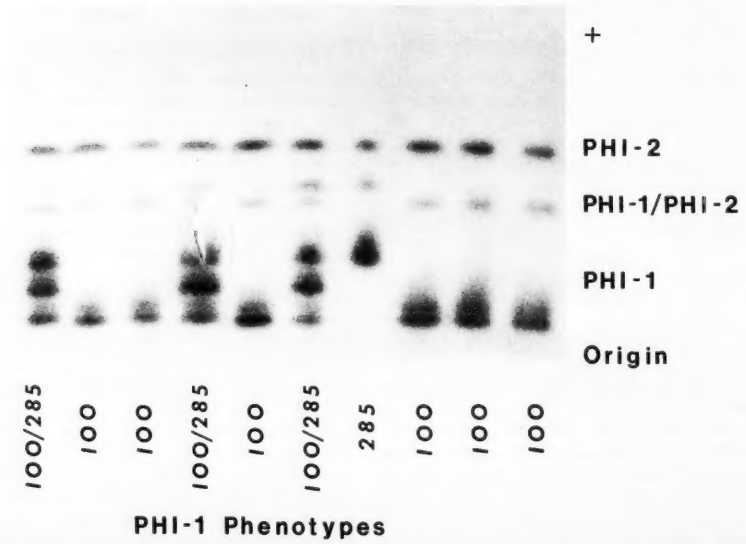

FIG. 4. Representative phosphohexose isomerase phenotypes. Faint, secondary bands produced by repeated freezing and thawing of samples can be seen slightly anodal to each of the PHI-1 bands. Note the presence of heterodimer bands.

from the primary bands. These observations are consistent with the 2-locus, dimer model of phosphohexose isomerase proposed for other fish species (Dando 1974; Johnson 1977; Place and Powers 1978; Smith and Jamieson 1978; Utter and Folmar 1978). Loci and alleles were named according to the conventions described in Allendorf and Utter (1979).

In muscle tissue, MDH gave a consistent three-banded pattern, with the intermediate band somewhat fainter than the other two. Only the slow band was evident in liver, while heart showed the slow band and a fainter intermediate band. These observations are consistent with the hypothesis of two malate dehydrogenase loci with dimeric structure and a heterodimer band. The fast locus, MDH-2, is most active in muscle, while the slow locus, MDH-1, is most active in liver. One individual from the Bering Sea was heterozygous at MDH-2 and showed a typical 3-banded pattern plus two MDH-1/MDH-2 heterodimer bands. All other individuals were homozygous. Repeated freezing and thawing produced a blurring of bands and a reduction in overall activity, but no secondary bands were produced. These observations of MDH activity and structure are consistent with observations from other fish species (Numachi 1970; Clayton et al. 1971; Karig and Wilson 1971; Clayton et al. 1973). Because only one individual was heterozygous at either MDH locus, MDH is not considered a polymorphic locus for the following analyses. It does, however, contribute to the genetic distance calculations in comparisons of the Atlantic and Bering Sea samples.

The following 13 loci were examined and found to be monomorphic in all samples: superoxide dismutase (SOD), aspartate amino transferase (AAT-1 and AAT-2), malate dehydrogenase (MDH-1), lactate dehydrogenase (LDH), glucose-6-phosphate dehydrogenase (GPDH), glutamate dehydrogenase (GDH), malic enzyme, isocitrate dehydrogenase (ICDH-1 and ICDH-2), xanthine dehydrogenase (XDH), sorbital dehydrogenase (SDH), and phosphohexose isomerase (PHI-2).

To test the genetic models further for the two polymorphic loci, PGM and PHI, the samples from each trip were analyzed for possible effects of sex, age, or degree of sexual maturity on phenotype and allele frequencies. No significant effects were found. The observed phenotype frequencies were then compared with those expected according to the Hardy–Weinberg distribution. (Rare alleles were combined for these comparisons.) The results of these comparisons are given in Table 1 and indicate a very close agreement with Hardy–Weinberg expectations for both loci, with no consistent trend in the slight deviations from expected. This evidence strongly supports the genetic models of isozyme variability at the PGM and PHI loci.

Having tested the validity of the genetic models of isozyme variability at the PHI and PGM loci, I next examined this variability in light of the three a priori hypotheses concerning population structure. The first of these hypotheses was that the Greenland halibut from the banks and slopes of Labrador and Newfoundland (NAFO subareas 2 and 3) should form a single, genetically homogeneous stock or population. To test this hypothesis, I compared PHI and PGM allele frequencies from the three Northwest Atlantic samples (Tables 2 and 3). No significant heterogeneity was found among these areas for either PGM ($\chi^2 = 1.78$, df = 6, $P > 0.50$) or PHI ($\chi^2 = 3.24$, df = 6, $P > 0.50$) (rare alleles were combined for the statistical comparisons).

As a second test of this hypothesis, all three Northwest Atlantic samples were combined and the observed phenotype distribution in this combined sample was compared with that expected according to the Hardy–Weinberg law assuming a single panmictic population. A deficiency of heterozygotes in the combined sample would suggest heterogeneity within the sample. No such heterozygote deficiency was evident for either PGM ($\chi^2 = 0.117$, df = 3, $P > 0.50$, $F = -0.008$), or PHI ($\chi^2 = 2.734$, df = 3, $P > 0.40$, $F = -0.009$). Thus, the first a priori hypothesis, that of homogeneity among Northwest Atlantic stocks, cannot be rejected.

The second a priori hypothesis was that Greenland halibut from the Gulf of St. Lawrence form a separate breeding unit and therefore should differ genetically from the Northwest Atlantic stock. The allele frequencies at both loci in the Gulf sample clearly differ more from those in the Northwest Atlantic samples than the latter do from each other (Tables 2 and

TABLE 1. Results of χ^2 comparisons of observed and expected phenotype distributions for PGM and PHI-1.

Locus		Sample				
		Northwest Atlantic			Gulf of St. Lawrence	Bering Sea
		1	2	3		
PGM	N	268	295	215	94	52
	χ^2	0.504	1.469	0.387	1.008	0.497
	df	2	2	2	2	2
	P	>0.50	>0.40	>0.50	>0.50	>0.50
	F[a]	0.03	−0.03	−0.04	0.07	0.05
PHI-1	N	257	295	215	94	51
	χ^2	1.457	0.439	1.059	1.555	5.922
	df	2	2	2	2	2
	P	>0.40	>0.50	>0.50	>0.40	>0.30
	F[a]	−0.06	0.03	−0.005	0.03	−0.05

[a] $F = 1 - (H_o/H_e)$ where H_o is the observed number of heterozygotes and H_e is the expected number.)

TABLE 2. Allele frequencies for PGM.

	Sample				
	Northwest Atlantic			Gulf of	Bering
Allele	1	2	3	St. Lawrence	Sea
100	0.808	0.807	0.816	0.787	0.529
112	0.144	0.146	0.126	0.149	0.413
125	0.045	0.042	0.051	0.064	0.048
140	0.002	0.003	0.002	—	0.010
70	—	0.002	0.005	—	—
90	0.002	—	—	—	—
N	268	295	215	94	51

TABLE 3. Allele frequencies for PHI-1.

	Sample				
	Northwest Atlantic			Gulf of	Bering
Allele	1	2	3	St. Lawrence	Sea
100	0.726	0.725	0.723	0.713	0.304
214	0.043	0.046	0.042	0.064	0.245
285	0.220	0.224	0.219	0.197	0.392
0[a]	0.012	0.005	0.014	0.011	0.019
−150	—	—	0.002	0.016	—
60	—	—	—	—	0.019
310	—	—	—	—	0.019
N	257	295	215	94	51

[a]This allele did not migrate significantly from the origin. In this instance, 0 does not designate a silent allele.

3). However, the difference between the Gulf sample and the pooled Northwest Atlantic samples is not significant for either PGM ($\chi^2 = 0.76$, df = 2, $P > 0.50$) or PHI ($\chi^2 = 5.55$, df = 3, $P > 0.10$). Further, pooling of the Gulf sample with the Northwest Atlantic sample gives no indication of a Wahlund effect (heterozygote deficiency) for either PGM ($\chi^2 = 1.389$, df = 3, $P > 0.50$, $F = 0.008$) or PHI ($\chi^2 = 0.672$, df = 3, $P > 0.50$, $F = -0.002$). However, for these comparisons it was necessary to pool rare alleles, thus masking the contribution of rare allele frequencies to differences between the Gulf and Northwest Atlantic areas. In particular, the rare allele, *PHI*--150, occurs at a much higher frequency in the Gulf than in the Northwest Atlantic (the overall frequency here is only 0.0007) (Table 3). This difference is highly significant ($\chi^2 = 10.97$, df = 1, $P < 0.001$) when only the frequency of this allele is compared between the two groups. Thus, the common allele frequencies at both loci and the significant difference in frequencies of *PHI*--150 suggest that Greenland halibut from the Gulf of St. Lawrence differ more from Northwest Atlantic samples than the latter do from each other. However, the lack of statistical significance in the common allele frequency differences and the presence of *PHI*--150 in the Northwest Atlantic-3 sample indicate that the populations in these two areas are not completely isolated. The presence of *PHI*--150 in the Northwest Atlantic-3 sample but not in the more southern Northwest Atlantic-2 sample suggests that gene flow (i.e. migration) may occur through the Strait of Belle Isle rather than through the Gulf of St. Lawrence to the Grand Bank area. A comparison of the relative similarity of common allele frequencies (rare alleles pooled) between the Gulf and the three Northwest Atlantic areas confirms this hypothesis (Table 4): although no obvious pattern emerges from the comparisons at the PGM locus, PHI allele frequencies in the Gulf sample are most similar to those from the Northwest Atlantic-3 sample, and differ most from the Northwest Atlantic-2 sample. These results thus suggest a Gulf stock which is relatively isolated from the Northwest Atlantic stock but with some gene flow occurring between the two, probably through the Strait of Belle Isle.

The third a priori hypothesis was that Greenland halibut from the Bering Sea differ genetically from Atlantic Greenland halibut. A corollary of this hypothesis is that the difference between Bering Sea and Atlantic samples should be greater than the differences among Atlantic samples. A comparison of allele frequencies in the five samples (Tables 2 and 3) suggests that this hypothesis is correct. Statistical comparisons of the Northwest Atlantic, Gulf and Bering Sea samples confirm this (Table 5). The presence of two unique PHI alleles (*PHI*-60 and *PHI*-310) in the Bering Sea sample is further evidence of the difference between Atlantic and Bering Sea Greenland halibut.

To estimate the degree of taxonomic divergence between Greenland halibut in the Atlantic (including the Gulf) and those in the Bering Sea, I calculated Nei's standard genetic distance between the samples from the two regions (Nei 1972, 1976, 1978). The allele frequencies at all 16 loci assayed were

TABLE 4. Relative similarity of allele frequencies in the Gulf and Northwest Atlantic samples.

Locus	Comparison	χ^2	df	P	C[a]
PGM	Gulf × Northwest Atlantic-1	0.72	2	>0.50	0.032
	Gulf × Northwest Atlantic-2	0.82	2	>0.50	0.032
	Gulf × Northwest Atlantic-3	0.75	2	>0.50	0.035
PHI	Gulf × Northwest Atlantic-1	3.59	3	>0.30	0.071
	Gulf × Northwest Atlantic-2	7.85	3	<0.05	0.100
	Gulf × Northwest Atlantic-3	2.33	3	>0.50	0.061

[a]Contingency coefficient = $[\chi^2/(\chi^2 + N)]^{1/2}$.

TABLE 5. Relative similarities of allele frequencies among Atlantic and Bering Sea samples.

Locus	Comparison	χ^2	df	P	C[b]
PGM	Total Atlantic[a] × Bering Sea	56.60	2	<0.0005	0.172
	NW Atlantic × Bering Sea	56.53	2	<0.0005	0.181
	Gulf × Bering Sea	25.74	2	<0.0005	0.285
	NW Atlantic × Gulf	0.76	2	>0.50	0.030
PHI	Total Atlantic[a] × Bering Sea	118.15	3	<0.0005	0.247
	NW Atlantic × Bering Sea	122.01	3	<0.0005	0.263
	Gulf × Bering Sea	47.77	3	<0.0005	0.376
	NW Atlantic × Gulf	5.55	3	>0.10	0.057

[a]Total Atlantic = Northwest Atlantic plus Gulf of St. Lawrence.
[b]Contingency coefficient = $[\chi^2/(\chi^2 + N)]^{1/2}$.

included in these calculations. These data yielded a standard genetic distance of 0.098. This value is considerably larger than is typically observed between local races or subpopulations of vertebrates, but is well below values typical of divergence on the species level (Nei 1972, 1976, 1978; Avise 1976). It suggests a taxonomic status of subspecies, and a divergence time of ~500 000 years (Nei 1976, 1978). However, since all of the proteins used for this comparison can be expected to accumulate amino acid substitutions relatively slowly (Sarich 1977), the foregoing estimates of degree of taxonomic divergence and divergence time will tend to be conservative. According to Sarich (1977), a genetic distance of 0.098 based upon only slowly evolving proteins, as in this study, would reflect a divergence time of ~3 million years. Thus, the electrophoretic evidence suggests a considerable degree of reproductive isolation between Atlantic and Bering Sea Greenland halibut. While the resulting evolutionary divergence has not yet reached the species level, it is well beyond the range normally associated with subpopulations or stocks, and indicates that the Greenland halibut from the two oceans could be appropriately classified as distinct subspecies of *Reinhardtius hippoglossoides*.

Discussion

The above electrophoretic analysis has confirmed all three of the a priori hypotheses concerning population structure in Greenland halibut. Greenland halibut show no detectable genetic heterogeneity along the slopes and banks of Labrador and Newfoundland. There is no reason, therefore, to doubt the hypothesis that this broad area contains a single, interbreeding stock. Other evidence supporting this hypothesis has come from the distribution of Greenland halibut by age and maturity (Bowering 1978), observed patterns of adult migration (Pitt 1974) and of larval drift and distribution (Templeman 1973), and vertebral numbers (Templeman 1970). Similar evidence suggests that this stock extends north to Baffin Island and West Greenland (Jensen 1935, Smidt 1969; Templeman 1970), but there is no electrophoretic evidence to bear on this.

Evidence of a separate breeding population of Greenland halibut in the Gulf of St. Lawrence comes from direct evidence of mature individuals (Templeman 1970; Lear 1970), and from significant differences in vertebral number between Gulf Greenland halibut and those from other areas of the Northwest Atlantic (Templeman 1970). More recently an analysis of Greenland halibut landings in the Gulf (Bowering 1980) has revealed that the Gulf catch is dominated by the year-classes which have shown exceptional strength in NAFO areas 2J3K. Further, the rate of recruitment to the Gulf fishery has exceeded that which could be produced by the standing stock of mature fish within the Gulf. These observations have led the assessment biologists to postulate some recruitment to the Gulf from the Labrador–Northeast Newfoundland area by way of migration through the Strait of Belle Isle (Bowering 1980). The electrophoretic evidence supports this hypothesis, indicating a separate breeding area in the Gulf, but with some gene flow (migration) between the Gulf stock and the northeastern Newfoundland area, probably through the Strait of Belle Isle.

The electrophoretic results suggest that Greenland halibut from the Bering Sea differ significantly from Atlantic Greenland halibut, and that the degree of genetic divergence between these regions greatly exceeds that between the Gulf of St. Lawrence and Northwest Atlantic stocks, being on the order of subspecies rather than stocks. An analysis of ver-

tebral number in these three regions revealed a similar pattern (Templeman 1970): the average difference between Northwest Atlantic and Pacific Greenland halibut (~ 1 vertebra) is close to 4 times as great as the average difference between Northwest Atlantic and Gulf samples. Separation of Atlantic and Pacific Greenland halibut at the subspecific level was suggested previously by Vernidub and Panin (1937, from Hubbs and Wilimovsky 1964) on the basis of morphometric comparisons. However, Hubbs and Wilimovsky (1964) found little difference between Atlantic and Pacific Greenland halibut in a survey of morphometric and meristic characters, including vertebral number. They reject subspecific status, believing that genetic differentiation between the two ocean areas has not proceeded beyond the racial level. Thus, although it is generally agreed that the variability in Greenland halibut between oceans exceeds that within either ocean, the degree of divergence found between oceans varies from study to study. Our hypothesis of divergence on the subspecific level can be confirmed only through a more comprehensive comparison of all three types of data using large samples from both oceans.

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Optimum Escapements in the Face of Alternative Recruitment Hypotheses

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Available data are often inadequate to discriminate among alternative models that make different predictions about the consequences of allowing escapements outside the range of recent historical experience. Dynamic programming is used to show that the optimum policy in such situations can involve active probing or experimentation with escapements. The optimum adaptive policy is usually difficult to compute, but generally may be closely approximated by a "Bayes equivalent" policy that is simpler to estimate but does not account explicitly for the value of information associated with allowing more extreme escapements. While there are various practical difficulties in estimating and implementing an optimum policy, it is concluded that regular probing experiments should be included in every fishery management plan.

Key words: stock-recruitment, optimization, adaptive management, stochastic models

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Souvent, les données dont on dispose ne permettent pas de différencier entre modèles donnant différentes prévisions quant aux conséquences d'échappements situés en dehors de la gamme observée dans un passé récent. Une programmation dynamique permet de démontrer que dans de telles situations, la politique optimale peut comporter sondage ou expérimentation active impliquant plusieurs échappements. Il est ordinairement difficile de calculer une politique adaptive optimale, mais on peut généralement s'en rapprocher au moyen d'une politique d' « équivalent Bayes » , plus simple à estimer mais qui n'explique pas clairement la valeur de l'information obtenue par l'adoption d'extrêmes d'échappements plus étendus. Bien qu'il soit difficile, à divers degrés, d'estimer et d'appliquer une politique optimale, nous sommes d'avis que tout plan de gestion des pêches devrait inclure expérimentation régulière.

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A prevailing myth in resource management theory is that one should construct a model that best reflects available data, then operate as though this model were correct. Errors are supposed to reveal themselves in due course and lead eventually to better models. Thus we see "best" estimates of maximum substainable yields (MSYs), total allowable catches (TACs), optimum equilibrium yields, and optimum fixed escapements. Luckily fisheries managers have never taken these estimates very seriously; when not constrained to do otherwise by political or economic circumstances, managers have behaved with a sensible balance of caution and (on occasion) deliberate experimentation. Recent work in adaptive control theory indicates that such managers have behaved correctly at least in a qualitative sense, and that the "best model" myth is far from optimal.

This paper attempts to show that fisheries managers should, in theory as well as practice, behave in an actively adaptive manner. They should not accept any single model as best, and should not be locked into equilibrium policies of any sort. Often they should actively probe the managed system through deliberate manipulation of harvest rates, or at least act with a balance of caution and optimism that has the same effect. To simplify the following discussion, the problem of choosing optimum escapements for fish like salmon will be used as a case example; the basic conclusions apply directly to other fisheries contexts.

The concept of adaptive or experimental management has strong intuitive appeal for fisheries scientists, but it is not obvious how to design policies for practical situations. It is easy to confuse scientific curiosity with a real need for better management information. Experiments usually involve giving up harvest later (reduced escapements) to provide a better basis for long-term harvesting; the appropriate balance of harvest costs and benefits is difficult to estimate. It is not clear whether experiments should involve large disturbances for a short time, or smaller (incremental) changes over long periods. There have been attempts to compare alternative experimental schemes using simple tools from statistical decision theory (Walters and Hilborn 1976; Walters 1977), and to find

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optimal policies (experimental or not) using methods from stochastic control theory (Silvert 1978; Mendelssohn 1980); the latter approach will be developed further in this paper.

Adaptive Management as an Optimization Problem

This section presents a somewhat involved analysis of optimum policies in the face of uncertainty. To motivate what follows, I ask the reader to place himself in the position of a decision maker faced with a prototype of the problem that the mathematics will address. Suppose he is trying to manage a salmon population and wishes to know what spawning stock to allow. Suppose his basic objective is simply to maximize the long-term harvest, with future catches discounted at some rate. Since the long-term harvest is not predictable (if for no other reason than unpredictable environmental effects on recruitment), he is willing to accept a policy that maximizes its expected value across some probability distribution of possible outcomes.

Now suppose he has two scientific advisors who have analyzed historical stock/recruitment data for the population (or one advisor and a critic hired by the fishing industry), each with the objective of developing a model to predict average recruitment as a function of the spawning stock decision. The advisors have come up with two different models (Fig. 1) that are consistent with recent historical experience but make different predictions about the consequences of allowing high spawning stocks. The first advisor predicts that recruitment would increase greatly if more fish were allowed to spawn (model M_2 in Fig. 1), and he argues for the spawning stocks S_2^*. The second advisor (or critic) arrives at model M_1 of Fig. 1, which implies that the spawning stock should be kept low.

The decision maker has at least five possible reactions to this situation. First, he may simply ignore the analysts and rely on his intuition, which usually just means trying to maintain the same escapement as in recent years. Second, he may invest in a research project aimed at deciding what model is correct, and try to maintain historical escapement levels while waiting for its results. The trouble with this approach is that the predictions resulting from the research can only be finally validated by actually manipulating escapements; thus the research will most likely just delay the difficult decision. Third, he may weigh the evidence and judge which model looks best to him personally (in terms of his own experience), then operate as though that model were correct. Walters and Hilborn (1978) and others have termed this a "passive" adaptive approach; if he judges in favor of M_2, he will accidentally do an experiment (choose S_2^*) that will show which model in Fig. 1 is correct. But if he initially judges in favor of M_1, he will learn nothing and perhaps miss a grand opportunity for increased future stock and harvest. Fourth, he may admit both models to the analysis by weighing possible outcomes according to a priori odds placed on the two models, but not account in his calculations for the effect of his decision on uncertainty about which model is correct. He may assume that uncertainty will change in the future, but not view the changes as dependent on his policy. Following Mendelssohn (1980), I will call the best policy that can be computed with this approach the "Bayes equivalent" policy. Fifth, he may attempt a full-

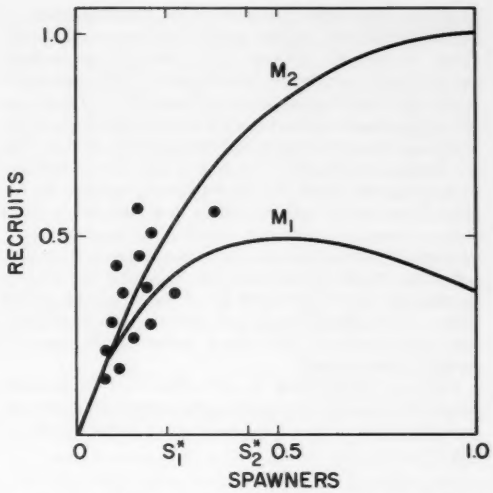

FIG. 1. Uncertainty about equilibrium stock size expressed as two alternative hypotheses (Ricker curves in this example), for a hypothetical data set. S_1^* is the stochastic optimum spawning stock if M_1 is known to be true; S_2^* is the optimum if M_2 is true.

decision analysis of the problem, according to a procedure such as described in this section. This analysis will (1) admit both (or many) models as possible outcomes in weighing his expectations of future yields; (2) account for effects of his decision on learning about which model is correct, and thereby account for the legacy of uncertainty (and possible lost yields) that he leaves for decision makers in the future; and (3) account for effects of unpredictable environmental variation on yields and on learning. The policy resulting from this analysis is called "actively adaptive," since it may involve deliberate or active variation of spawning stocks to learn faster.

Having chosen a passive adaptive, Bayes equivalent, or active adaptive approach, the decision maker might next try to enumerate the possible future consequences of each decision open to him. He will then see a "branching tree" of possible stock sizes and decisions, growing geometrically into the future; forward (in time) evaluation of possible policies is hopelessly complex in systems subject to stochastic variation. Fortunately, the branching tree can be represented in a computational framework that does not grow explosively over time, namely stochastic dynamic programming (Bellman 1961). For typical harvesting problems, this formulation also results in a remarkable bonus: it shows that the optimum decision can be expressed as a feedback function of the system state, independent of time (provided the manager does not have a very short time horizon of a few fish generations). The feedback policy specifies what to do (what escapement to allow) for any state (stock size) that occurs, without assuming that the manager can predict this state in advance.

Dynamic Programming Formulations

The remainder of this section develops stochastic dynamic programming equations for actively adaptive management.

There has been some confusion in the literature about the correct formulation, so this section will present it in some detail. Walters and Hilborn (1976) presented an incorrect and deceptive formulation; Mendelssohn (1980) presented a Bayes equivalent formulation as defined above. The correct formulation has been developed for other problems by various authors in the control theory literature (Bryson and Ho 1965; Bar Shalom and Tse 1976; Tse et al. 1973). For readers who wish to skip the details and see numerical examples, the key point of the analysis will be to show how optimum feedback policies depend on a decision maker's "information state," measured by probabilities he places on alternative models (or parameter values). For example, we will want to show how the decision maker faced with Fig. 1 should choose escapements as a (feedback) function of stock size and the information state measure P_t, the current probability he places on model 1 being correct.

Dynamic programming is most often used for problems where one desires to maximize a discounted sum of periodic payoffs (i.e. harvests) across a sequence of decision points, or stages:

$$(1) \quad \text{maximize } V_T = \sum_{t=T}^{N} \lambda^{t-T} v_t.$$

Here V_T is the total return from stage (i.e. time step) T forward to an end time N, λ is a discount factor ($\lambda \leq 1$; $\lambda = 0.9$ would mean a 10% discount rate), and v_t is the payoff in stage t. Bellman's "principle of optimality" is based on recognizing that (1) can be written recursively:

$$(2) \quad V_T = v_T + \lambda V_{T+1}$$

(i.e. the total return is an immediate payoff plus a long-term return). Suppose one has alternative decisions s_t that might be applied at stage t, and a model for how some set of state variables $\mathbf{x}_t = (x_1, \ldots, x_n)_t$ will affect the short-term payoff and will in turn be affected by the decision:

$$(3) \quad \begin{aligned} v_t &= v_t(\mathbf{x}_t, s_t) \\ x_{i,\,t+1} &= f_i(\mathbf{x}_t, s_t) \qquad i = 1, \ldots, n. \end{aligned}$$

For example, if $x_1 = R_t$ = this year's stock size and s_t = number of spawners allowed, then we might take the catch as a simple payoff measure; then $v_t(R_t, s_t) = R_t - s_t$. $f_1(\mathbf{x}, s)$ would be a stock recruitment model. Equation (3) implies that the variables in equation (2) should be written as functions of $\mathbf{x}$ and s; the principle of optimality then says that the maximum value of V_T, say V_T^*, can be written as

$$(4) \quad V_T^*(\mathbf{x}_T) = \underset{\text{choices of } s_T}{\text{maximum over}} \; [v_T(\mathbf{x}_T, s_T) + \lambda V_{T+1}^*(\mathbf{x}_{T+1})].$$

In words, the best return that can be obtained from time T forward for any state $\mathbf{x}_T$ is found by choosing that s_T which will maximize the combined short-term (v_T) and long-term (V_{t+1}) returns; the long-term return depends on s_T in that the next system state ($\mathbf{x}_{T+1}$) depends on it (eq. 3). The same formulation is used for stochastic problems, except that the goal becomes to maximize expected total returns across a collection of possible outcomes that can each be assigned some probability of occurring.

Suppose uncertainty involves two components: "random environmental effects" w_t that may alter $\mathbf{x}_{t+1}$ no matter what decision s_t has taken, and a pair of alternative hypotheses $f_1^{(1)}$ and $f_1^{(2)}$ about the dynamics of the state variable x_1. If x_1 is stock size R_t, we might for example wish to admit the two alternative recruitment hypotheses shown in Fig. 1. If we then try to ask "what spawning stock will maximize the expected short term plus long term yield," we will have to place odds on the two alternative hypotheses as well as on the various tricks w_t that nature may play. More formally, at any time T the decision maker must base his decision not on which hypothesis is true, but rather on his current "information state" (R_T, P_T), where R_T is stock size and P_T is the probability he places on model $f_1^{(1)}$ being correct given the data available to him at time T (the probability of $f_1^{(2)}$ is then $1 - P_t$ if he admits only two alternatives; for what follows we shall assume that he can assess R_T accurately before choosing s_T). Restating this argument in terms of the principle of optimality (eq (4)), he should make that decision $\hat{s}_T$ which maximizes an expected value $\hat{V}$ which weighs the two possible models according to the information state:

$$(5) \quad \begin{aligned} \hat{V}_T(R_t, P_T) = v(R_T, s_T) &+ P_T \underset{w_T}{\mathscr{E}} V_{T+1}^*(R_{T+1}, P_{T+1}, f_1^{(1)}) \\ &+ \lambda(1 - P_T) \underset{w_T}{\mathscr{E}} V_{T+1}^*(R_{T+1}, P_{T+1}, f_1^{(2)}). \end{aligned}$$

Here $\underset{w_T}{\mathscr{E}} V^*(R, P, \theta)$ is to be read "the expected long term value across possible environmental outcomes w_t, given that θ is the correct model but that the decision maker's information state about it will be P_{t+1}." Notice that these conditional long-term values depend not only on which model is actually correct, but also on the information state $\{R_{T+1}, P_{T+1}\}$ that results from the decision at time T; the decision maker at $T+1$ will also have to choose a $\hat{s}_{T+1}$ that has uncertain consequences. In other words, the decision maker at time T leaves his successor with a legacy of uncertainty, measured by P_{T+1}, and he should (in a value maximizing sense) account for this in his assessment of V_{T+1}.

Though the decision maker cannot, with the information at his disposal, do better at time T than to choose the $\hat{s}_T$ that maximizes equation (5), his long-term value from time T forward depends on which model is correct:

$$(6) \quad V_T^*(R_T, P_t, \theta) = v(R_T, \hat{s}_T) + \lambda \underset{w_t}{\mathscr{E}} V_{T+1}^*(R_{T+1}, P_{T+1}, \theta)$$

where R_{T+1} and P_{T+1} depend on P_T, w_T, R_T, $\hat{s}_T$, and θ. V_T^* depends on P_t because $\hat{s}_T$ depends on P_t (see eq. 5). Equation (6) is in the recursive format of dynamic programming, and a sequence of optimal decisions $\hat{s}_N, \hat{s}_{N-1}, \ldots \hat{s}_T$ can be found for alternative states R, P, and θ by working backwards in time from a terminal value function $V_N^*(.)$ or by "policy iteration" if N is infinite. Generally $\hat{s}$ becomes independent of t after a sufficient number of backward iterations; it is then a function only of R and P, and is called a stationary feedback policy. Equations (5) and (6) differ from many textbook presentations of dynamic programming (eq. 4) in that $\hat{s}_t$ is not a function of the whole state $\{R_t, P_t, \theta\}$ but only of the information state $\{R_t, P_t\}$. There need be no presumption that the decision maker can

assess P_t in some optimal way given the data available. However, it is required that P_{t+1} be computable only from R_t, P_t, θ, and w_t; it must be treated as a sufficient statistic for the past data (otherwise each past observation would have to be included as a component of the information state).

Equations (5) and (6) can be generalized to cases where many alternative hypotheses are admitted, though the dynamic programming computations soon become practically impossible. An example where numerical calculations are feasible is the set of hypotheses generated by allowing the β parameter of the Ricker recruitment model to vary

$$(7) \quad f_t^{(i)} = s_T e^{\alpha - \beta_i s_T} + \sigma w_T$$

where s_T is the spawning stock decision in state T, α is a production parameter, and w_T is a normally distributed environmental effect with mean 0 and variance 1. Beta can take an infinite number of values, but a dynamic programming solution can be obtained if the decision maker's information state about β can be compressed to a distribution $p_T(\beta)$ characterized at time T only by its mean $\hat{\beta}_T$ and variance $\sigma^2_{\hat{\beta}}$ ($\hat{\beta}_T$ and $\sigma_{\hat{\beta}}$ are information state measures analagous to P_t in the two-model case.) As a generalization of equation (5), we should choose that $\hat{s}_T$ which maximizes

$$(8) \quad \hat{V}_T(R_T, \hat{\beta}_T, \sigma^2_{\hat{\beta}}) = v(R_T, s_T) + \lambda \int_{\beta} p_T(\beta) \mathop{E}_{w_T} V^*_{T+1}(R_{T+1}, \hat{\beta}_{T+1}, \sigma^2_{\hat{\beta}_{t+1}}, \beta)$$

and the returns that he achieves will propagate as in equation (6) with β replacing θ. The integral in equation (8) simply represents taking the expected value of V^*_{T+1} across the probability distribution of β at time T. Walters and Hilborn (1976) incorrectly supposed that equation (8) could be solved recursively without including the true β as a dimension of V^*_T; the effect of that error was to make the decision maker appear able to manipulate the true β (by choosing s_T values that would quickly reduce $\sigma^2_{\hat{\beta}}$ upon encountering a favorable estimate $\hat{\beta}$).

The Dual Effect and Probing Policies

The value equations (5) and (8) contain no explicit terms to account for value of information or reduced uncertainty. But consider the effect that P_T has on the choice of an optimum $\hat{s}_T$ in equation (5). If P_t is not close to 0 or 1, the best choice will reflect a weighting of possible outcomes. If s_1^* is the optimum decision given that model 1 is known to be true, and s_2^* is the optimum given model 2, then the weighting of equation (5) will often place $\hat{s}_t$ between these extremes. If nothing else, $\hat{s}_T$ will reflect caution in case the less-productive model is true. In short, $\hat{s}_T$ will not be optimum for either model, and this problem will be reflected in $V^*_T(R_T, P_T, \theta)$ for both values of θ. For many dynamical situations, nothing can be done about the problem; either future learning is not possible ($P_{t+1} = P_t$ for all $t > T$), or learning takes place at rates independent of s_t (P_{t+1} not a function of $\hat{s}_T$). Mendelssohn (1980) notes for example that the Bayes equivalent formulation leads to an optimum policy for the Ricker model when β is known but α is unknown; in this case learning rate is independent of s_t. Learning rates are independent of decisions in the "linear-quadratic" systems that have been analyzed extensively in the control theory literature (Bar Shalom and Tse 1976). Silvert (1978) notes that there are also cases when deliberate learning is possible but is not optimal.

For situations like Fig. 1, P_{T+1} can be influenced by the spawning stock choice s_T, and so therefore can V^*_{T+1}. This has been called the "dual effect of control." For small s_T, the decision maker at time $T+1$ will see a recruitment that is consistent with either hypothesis, and he will assign $P_{T+1} \simeq P_T$. For larger s_T, he will begin to see recruitments that are inconsistent with one or another hypothesis, and P_{T+1} will be larger or smaller than P_T; the exact gain in confidence will depend on the variance of environmental effects and/or sampling errors. This means that it is quite possible for the $\hat{s}_T$ that maximizes equation (5) to be larger than would be predicted by assuming $P_{t+1} = P_t$; the weighted average

$$P_t V^*_{t+1}(R_{t+1}, P_{t+1}, 1) + (1 - P_t) V^*_{t+1}(R_{t+1}, P_{t+1}, 2)$$

can be more sensitive to the changes in P_{t+1} produced by an increment in s_T than it is to changes in R_{t+1} produced by that increment, and this gain in long-term value can more than outweigh a short-term loss in $v(R_T, s_T)$. This argument is presented more formally in the Appendix.

If the optimum $\hat{s}_T$ does turn out to be different than predicted by assuming $P_{t+1} = P_t$, than we can reasonably call it a "probing" or "actively adaptive" decision. This is not to imply that the Bayes equivalent (assuming $P_{t+1} = P_t$) policy would not also result in rapid learning; but it is worth while to identify those situations where a special effort to learn rapidly will be worthwhile.

Bayes Theorem and The Dynamics of P_t

Bayes theorem provides a natural way to assign probabilities to alternative hypotheses, and it can be written in the recursive format needed for equations (5), (6), and (8). These equations then become a special case of "preposterior analysis" in statistical decision theory. The recursive form of Bayes theorem is

$$(9) \quad P_{T+1} = P(\text{model}|\text{new data}) = \frac{P(\text{new data}|\text{model})\, P(\text{model}|\text{old data})}{P(\text{new data})}.$$

Here the "prior probability" is $P_T = P(\text{model}|\text{old data})$. $P(\text{new data}|\text{model})$ is called the "likelihood" of the data given the model. $P(\text{new data})$ is a sum or integral of likelihoods times prior probabilities across all the models that have been admitted to the analysis. When there are no "old data", P_T represents a judgmental probability or degree of belief that can be assigned to the model on the basis of intuition or experience with other systems.

Equation (9) provides a complete characterization of uncertainty for two-model cases (e.g. Fig. 1) when two special assumptions are made: the environmental effects w_t must be statistically independent of one another, and the distribution of these effects (e.g. normal with mean 0.0 and variance σ^2_w) must be known a priori. In other words, the two models must be specified more completely than as a pair of curves; the expected distribution of data around the curves must also be

hypothesized in advance.

Suppose the two recruitment hypotheses in Fig. 1 are specified by

$$(10)\quad R_T^{(i)} = f^{(i)}(s_{T-1})\, e^{\sigma_w w_{T+1}} \qquad i = 1, 2$$

where $R_T^{(i)}$ is recruitment predicted by model i and $f^{(i)}$ is the recruitment curve. Suppose σ_w is assumed known, and w_{T+1} is assumed to be normally distributed with mean 0 and variance 1. Then the likelihood of any observation R_T given model i is

$$(11)\quad p(R_T/i) = \frac{1}{\sqrt{2\pi}\sigma_w} \exp\{-\frac{1}{2\sigma_w^2} \ln^2\left(\frac{R_T}{f^{(i)}(s_{T-1})}\right)\}$$

(i.e. $p(R_T|i)$ is the normal probability density evaluated for a deviation $\hat{w}$ that is derived from equation (10) with $R_T^{(i)} = R_T$). This likelihood can be substituted into Bayes theorem (equation 9), along with the corresponding likelihood for the other model, to provide updated assessments of P_T given P_{T+1}. Obviously, other distributions besides the normal could be assumed; the key requirement is to specify the distribution precisely for each recruitment hypothesis.

Bayes theorem rapidly becomes difficult to apply when many models are admitted to the analysis. If the alternative models represent different parameter values for a functional form that can be reformulated as a linear regression (i.e. α and β in equation (7) are linearly related to $\ln(R_T/s_{T+1})$), and if deviations from the regression are normally and independently distributed, and if the no-data prior is normal, then equation (9) results in recursive regression equations (see Walters and Hilborn 1976). The regression parameter estimates and their covariance matrix provide "sufficient statistics" from which the probability of any particular combination being correct can be computed. For the Ricker model equation (7) with only β unknown (and w_t normally distributed), the recursive linear regression equations are

$$(12)\quad \hat{\beta}_{t+1} = \hat{\beta}_t + \frac{\sigma_{\hat{\beta}_t}^2 s_t}{\sigma_w^2 + \sigma_{\hat{\beta}_t}^2 s_t^2}\{\alpha - \hat{\beta}_t s_t - \ln(R_{t+1}/s_t)\}$$

$$\sigma_{\hat{\beta}_{t+1}}^2 = \sigma_{\hat{\beta}_t}^2\left(1 - \frac{\sigma_{\hat{\beta}_t}^2 s_t^2}{\sigma_w^2 + \sigma_{\hat{\beta}_t}^2 s_t^2}\right).$$

The expectation over β in equation (8) is performed using $p_T(\beta)$ normally distributed with mean $\hat{\beta}_T$ and variance $\sigma_{\hat{\beta}_T}^2$. In equation (12), the ratio term involving $\sigma_{\hat{\beta}_t}^2$ is often called the "Kalman gain"; the bracketed term involving $\ln(R/S)$ is a prediction error and is often called the "innovation." Notice that $\sigma_{\hat{\beta}_{t+1}}^2$ is dependent on s_t; higher spawning stocks result in more rapid reduction in uncertainty about β.

Equations such as (12) can be reformulated to admit the possibility that system parameters are actually changing slowly over time. We would expect such changes in the Ricker parameter because of loss of spawning habitat, invasion of new spawning areas, loss of substocks, and so forth (Ricker 1973). The equation for $\sigma_{\hat{\beta}_{t+1}}^2$ can include a positive term to represent the possibility that β varies as a random walk; for uninformative s_t, $\sigma_{\hat{\beta}_t}^2$ can actually increase over time. Then, if the optimal policy calls for probing when $\sigma_{\hat{\beta}}^2$ is larger, the manager will regularly or occasionally be led to probe the system. In extreme cases, the optimum spawning stock can be a constantly varying quantity that never settles to any fixed value.

Computational Considerations

The optimization problem represented by equations (5) and (8) has so far defied analytical solution. Some approximate approaches have been suggested in the control literature (see review by Tse and Bar Shalom 1980); the promising "wide sense dual control algorithm" of Tse et al. (1973) has been used by Smith (1979) to study the Ricker and Schaeffer models. For prototype cases such as the two-model example in Fig. 1, or the Ricker model with one unknown parameter, dynamic programming can be used to approximate the optimal policy quite closely. This section reviews some numerical procedures and difficulties with such dynamic programming computations.

Numerical schemes for dynamic programming require that the value V_T^* of equation (4) be approximated as a function of the state variables $\mathbf{x}_t$; to accomplish this, the state variables are represented at discrete levels rather than as continuous quantities. Then two approaches are possible. The first is to structure the discretization such that every state transition $\mathbf{x}_t \rightarrow \mathbf{x}_{t+1}$ will go exactly to another (or the same) discretized point. Then each possible transition is assigned a probability and the problem is called a "Markov decision process." Mendelssohn (1979, 1980) has used this approach successfully for fisheries problems, and he cautions that the spawning stock decisions should be finely discretized (50 or more levels for some problems). The second alternative is to allow $\mathbf{x}_{t+1}$ to "miss" the discrete points where V_{t+1}^* has been computed (by backward recursion), then interpolate its V_{t+1}^* from the values at surrounding discretized points. One can get by with fewer discrete states using this alternative, but the interpolation procedure must be chosen carefully, especially when there are more than two state variables. Ludwig and Walters (1981b) have used an elaborate interpolation scheme to reduce radically the cost of computing the optimum policy for the Ricker model with β unknown. For adaptive problems, it appears most efficient to use a compromise between the two approaches.

Discretization usually results in an exploding computational problem as the number of state variables increases (Bellman's "curse of dimensionality"). If there are five x's, each of which is allowed 10 discrete levels, then V_T^* must be estimated at 10^5 points unless the system dynamics rule out some combinations. For the Ricker model with one unknown parameter β, the dynamic programming system state has four variables: R_t, $\hat{\beta}_t$, $\sigma_{\hat{\beta}_t}^2$, and β. If R_t is discretized at 100 levels, and the other variables at 10 levels each, one must compute V_t^* for 100 000 states. At each state, one must compute at least one expected value across environmental outcomes w_t and across the alternative models recognized in the information state. All this must be repeated for several stages T.

For either approach, the computations can be simplified considerably when the short-term payoff v_t is linear in the decision variable (Mendelssohn 1979). For example, $v_t = R_t - s_t$ when it is desired to maximize long-term catch and s_t is the spawning stock. In this case, the optimum s_t is a function only of V_{t+1}^* except for the constraint $s_t \leq R_t$. This means

that s_t will either be equal to R_t, or to some lower "fixed escapement" whose future value need not be recomputed for larger R_t after it has once been found by examining an increasing sequence of R_t levels. Usually the optimum fixed escapement will be the same for all $R_t \geq \hat{s}_t$. However, one can construct two-model adaptive problems where this is not true (i.e. a larger $\hat{s}$ may be optimal for sufficiently large R_t). In such cases it is necessary to compute the expected value of taking $s_t = R_t$ for every discrete R_t.

While the various computational difficulties outlined above make it very expensive to accurately compute optimal adaptive policies, it is fairly easy to determine whether the policies differ significantly from Bayes equivalent (passive learning) policies. In the dynamic programming backward recursion, the Bayes equivalent policy emerges as the optimum after the first recursive step (stage N-1), provided that the terminal value function $V_N(R_N, \ldots) = R_N$ for all values of its other arguments and provided $v(R, s) = R - s$. Then as the backward iteration proceeds ($T = N - 2$, $N - 3$, etc.), longer term-learning effects can begin to influence $\hat{V}_T$ and $\hat{s}_T$.

Numerical Examples

Estimates of optimal feedback policies for a few prototype examples should be helpful in designing heuristic policies for more complex situations that cannot be attacked with dynamic programming. This section will present dynamic programming results for three case examples: (1) the two-model uncertainty example of Fig. 1; (2) the two-model example shown in Fig. 2, where the manager knows something about recruitment at lower exploitation rates, but does not know how far the stock can be pushed before recruitment overexploitation occurs; (3) a parameter uncertainty example where the manager is willing to assume that the Ricker model is correct, but he has data only from low stock sizes and therefore does not have a good estimate of the equilibrium stock parameter β. For each of these cases, a variety of numerical solutions were obtained using different computation schemes.

A low discount rate ($\alpha = 0.98$) was used in all cases. This low discount rate reflects the author's presumption that fishery resources will generally be managed with long-term, resource husbandry objectives. This presumption is inherent in simple objectives such as MSY and the preservation of slow growing stocks such as marine mammals. It is also inherent in the willingness of governments to invest in fisheries research in general, and population dynamics studies in particular; catch, effort, age composition, and growth statistics are almost meangingless except in long-time series. Adaptive policy calculations weigh short-term cost (lost yield to generate higher escapement, etc.) against long-term gains through improved parameter estimates. Adaptive behavior will not be favored when the long-term gains are heavily discounted.

The following subsections dwell in some detail on various numerical problems. Readers wishing to skip the details can see the general results in Fig. 3–5 and Table 1, which compare adaptive optimal escapements to Bayes equivalent optimal escapements computed without accounting for future learning. Whenever uncertainty is high (probability on one model near 0.5, high σ_β^2), the optimum escapement is informatively higher or lower than the Bayes equivalent estimate. Judging

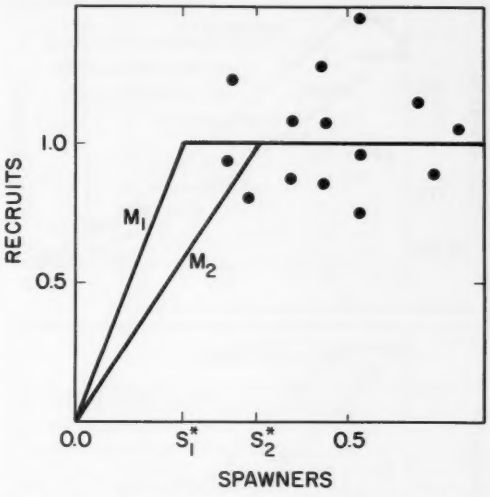

FIG. 2. Uncertainty about the maximum productivity of each spawner, expressed as two alternative recruitment curves, for a hypothetical data set. S_1^* is the optimum spawning stock if M_1 is true; S_2^* is the optimum if M_2 is correct.

from value functions computed in various tests, the optimum policy gives 1–5% improvements per year in long-term yields as compared to the Bayes equivalent policy.

Two Hypotheses about Equilibrium Stock Size

Figure 3 shows some estimates of the optimum escapement policy for the two-model problem of Fig. 1, and Bayes equivalent policies for the same discretization schemes. For these tests, the environmental variance σ_w^2 was assumed to be 0.04, and the optimum policy is shown for stage $N - 40$. Effects of increasing σ_w^2 with one discretization scheme are shown in Fig. 4. Estimates of the optimum policy are quite sensitive to the discretization of R_t, and are less sensitive to the discretization of P_t and w_t.

For fine discretization schemes (200 R_t levels, 40 P_t's, 20 w_t's), the optimum escapement was estimated to be higher than the Bayes equivalent policy for intermediate values of P_t. In other words, the optimum policy involves some active probing for information whenever there is high uncertainty about which model is correct. However, as noted by Mendelssohn (1980), the Bayes equivalent policies are very close to optimum. This is lucky because they can be computed much more cheaply. At stage $N - 40$ and for $P_t = 0.5$, the expected $\hat{V}$ (of eq. 5) for making the optimum decision was only 0.5% higher than for the Bayes Equivalent decision; the optimum "value of information" per decision is therefore very small. This difference was not detectable at all in discretization schemes involving less than 50 R_t levels, 20 P_t's, and 10 w_t's. The required number of P_t levels could be reduced considerably (to 10 or 2) by interpolating between levels; otherwise the effect of s_t on P_{t+1} was undetectable for many state transitions.

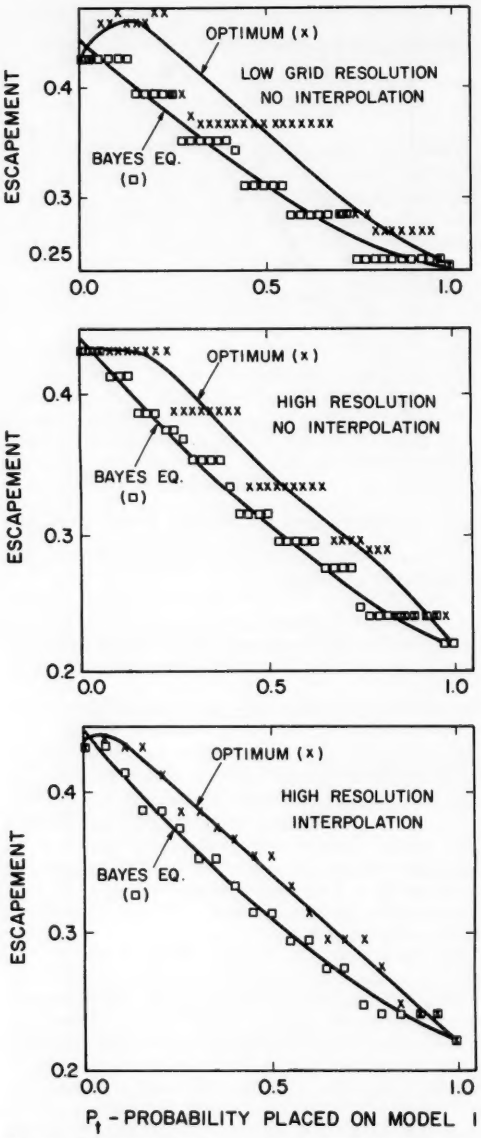

FIG. 3. Optimum and Bayes equivalent spawning policies estimated by dynamic programming for the two-model uncertainty problem of Fig. 1. Results are shown for three discretization schemes to illustrate the effect of increased resolution and interpolation. Freehand curves are meant to suggest how the optimum policy varies smoothly with P_t (in the absence of discretization effects). For the top panel, R_t was discretized at 150 levels, P_t at 41, and w_t at 10. For the middle panel, there were 200 R_t's, 41 P_t's, and 20 w_t's. For the bottom panel, there were 200 R_t's, 21 P_t's, and 20 w_t's. Compare also the bottom panel of Fig. 4.

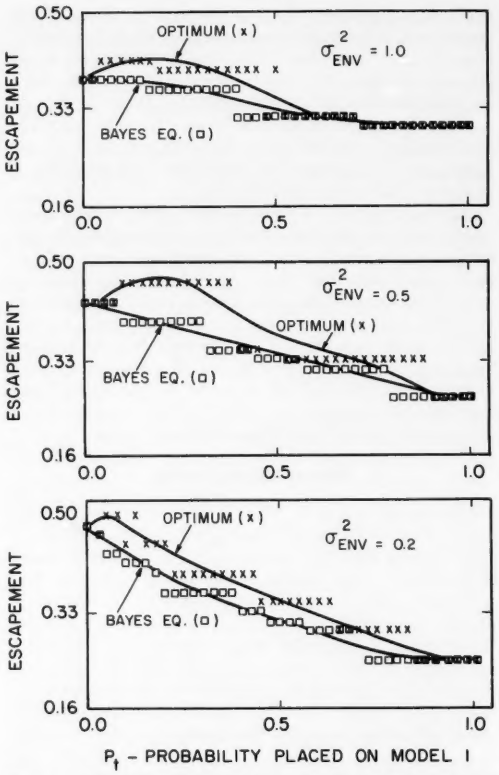

FIG. 4. Estimated optimum policies for the two-model problem of Fig. 1, for three assumptions about environmental variance around the mean stock–recruit curve. The freehand curves are to be interpreted as in Fig. 3. These results were computed with a coarse discretization scheme, without interpolation (100 R_t's, 41 P_t's, 20 w_t's).

A similar two-model problem (for Fraser River sockeye salmon) was analyzed by Walters and Hilborn (1976) and Walters (1977). Instead of computing the optimal feedback policy, they tested several "experimental," non-feedback policies involving high escapement for several years followed by sustained management according to whichever model was found to be correct during the experimental period. They concluded that moderate experiments are worthwhile for P_t near 0.5, and they likewise found the incremental value of probing to be very small.

HYPOTHESES ABOUT RECRUITMENT OVEREXPLOITATION

Figure 2 represents a classical problem in fisheries management: how low can the spawning stock be driven before recruitment begins to decline? A common management prescription in this situation has been to behave as though the more conservative model (M_2, lower maximum recruits/spawner) were correct, i.e. to avoid any risk of a recruitment

collapse. Questions of risk averse management will not be discussed here (see Mendelssohn 1979; Hilborn and Walters 1977; Keeney 1977; Walters 1977), but the results below indicate that a manager who simply wishes to maximize expected long-term catch should not behave in a highly conservative manner.

Estimated Bayes equivalent and optimal escapements for the problem are shown in Fig. 5. As in the previous example, σ_w^2 was assumed to be 0.04 and the optimum policy is for stage $N - 40$. The results can be interpreted very simply: unless the manager's confidence in the conservative hypothesis is very high (i.e. $P_t < 0.1$), he should behave as though the more optimistic hypothesis is correct. He should use a low spawning stock that is both highly informative, and also produces optimal yields if M_1 is correct.

For this example the Bayes equivalent and optimal policies are strikingly different; the Bayes equivalent policy is uninformative for $P_t < 0.6$. However, again only slight extra information value is achieved by using a smaller spawning stock. For $P_t = 0.5$, the optimum decision at stage $N - 40$ has an expected value 0.3% higher than the Bayes equivalent decision, assuming optimum decisions are taken after that stage. Figure 5 also shows that the optimum and Bayes equivalent policies need not vary smoothly with P_t and cannot be approximated by computing the optimum policy for a single "weighted model" that is intermediate between the two original hypotheses.

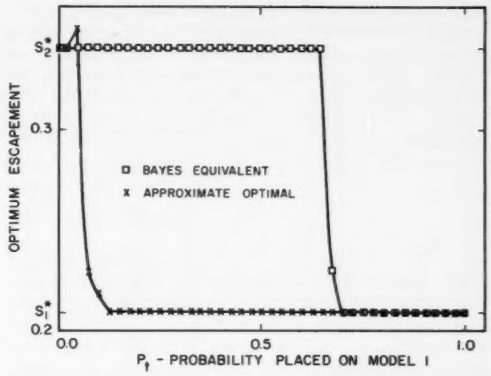

FIG. 5. Estimated Bayes equivalent and optimum spawning policies for the two-hypothesis problem of Fig. 2. The policies call for allowing escapements of S_1^* and S_2^* spawners, depending on P_t. The intermediate points near $P_t = 0.1$ and 0.7 are likely due to numerical inaccuracies. The policies were computed with 150 R_t levels, 40 P_t levels, and 20 w_t levels; interpolation was used for P_{t+1} between the discretized levels.

UNCERTAINTY ABOUT THE RICKER β PARAMETER

This example is an extension of the two-hypothesis case of Fig. 1, and the optimization problem is specified by eq. (7), (8), and (12). The question is, how should a manager behave if he wishes to admit great uncertainty about the equilibrium stock parameter β, and specifies his uncertainty through a normal prior distribution with mean $\hat{\beta}_0$ and variance $\sigma_{\hat{\beta}_0}^2$? For what follows, it will be assumed that he is confident that $\alpha = 1.0$ (see eq. 7) and $\sigma_w^2 = 0.04$.

The example raises severe numerical problems. The dynamic programming formulation has four state variables, and the optimal policy is difficult to distinguish from the Bayes equivalent estimate unless a fine discretization is used. Discretization of $\hat{\beta}$ and $\sigma_{\hat{\beta}_t}^2$ poses special problems. If the transitions $\hat{\beta}_t \rightarrow \hat{\beta}_{t+1}$ are forced to a few discrete levels of $\hat{\beta}_{t+1}$ (Markov decision formulation), it is difficult to choose the levels so that the estimator will be unbiased. Small changes in $\sigma_{\hat{\beta}_t}^2$ (associated with changes in s_t) are invisible for coarse discretizations. After various costly experiments, I achieved reasonably stable numerical results by discretizing R_t (and s_t) at 150 levels and the other variables at 10 levels. Linear interpolation was used to find V_{t+1}^* for values of $\hat{\beta}_{t+1}$ and $\sigma_{\hat{\beta}_{t+1}}^2$ that missed points on the discrete grid. The computations required massive computer storage (1 megabyte), and almost 5 min of CPU time for 20 backward iterations on the UBC Amdal system. The exercise would not be worth repeating in routine management contexts.

Another numerical and logical difficulty with the problem should be noted. If the prior distribution for β is normal, then eq. (12) implies that a wider range of $\hat{\beta}_t$ values should be included as possible outcomes as t increases. In other words, the discrete grid should grow in time, which would create some severe computational problems. By discretizing β and $\hat{\beta}$ on a fixed grid, it is tacitly assumed that the posterior distribution of β is not normal. Then eq. (9) may not provide sufficient statistics for the distribution, and the final result will not be Bayes optimal. Rather than deal with a growing grid, it was decided for this study to take $V^*(\hat{\beta} < \hat{\beta}_L) = V^*(\hat{\beta}_L)$ and $V^*(\hat{\beta} > \hat{\beta}_u) = V^*(\hat{\beta}_u)$ for fixed (discrete) bounds $\hat{\beta}_L = 0.01$ and $\hat{\beta}_u = 0.05$. The manager is envisioned as initiating each decision with a normal prior for β, then correcting exteme $\hat{\beta}$ estimates to the nearest acceptable bound (β_L or β_u): the values β_L and β_u are thus assigned higher probabilities of being correct than would be indicated by the normal prior.

Table 1 shows estimated Bayes equivalent and optimal spawning stocks (at stage $N - 20$), in integer levels, for a range of discrete $\hat{\beta}$ and $\sigma_{\hat{\beta}}^2$ values. The policies are indistinguishable except at high $\sigma_{\hat{\beta}}^2$, where the optimal policy calls for minor probing (higher spawning stocks). For small $\hat{\beta}$, the policies call for decreasing s_t as $\sigma_{\hat{\beta}}^2$ increases: this is due to the assumption that $\beta \geq \beta_L$: for high $\sigma_{\hat{\beta}}^2$, the policies are weighted by the possibility that $\beta > \beta_L$, but not by the reverse possibility. The opposite effect occurs for large $\hat{\beta}$: the analysis admits that β may be less than β_u (i.e. true optimum spawning stock may be higher), but not the reverse. For intermediate $\hat{\beta}$ levels, the Bayes equivalent policy approaches the "certainty equivalent" policy which would be to ignore $\sigma_{\hat{\beta}}^2$ and behave as if $\hat{\beta}$ were true.

As in the two-model case, the expected value of taking the optimal decision when $\sigma_{\hat{\beta}}^2$ is large is only slightly (0.1–0.5%) higher than the value of the Bayes equivalent decision. Probing is worthwhile though the expected contribution of each decision is small. Indeed, it is apparently less important to probe than it is to have an unbiased estimation procedure. Table 2 shows an estimated "optimum" policy computed while accidently rounding $\hat{\beta}_{t+1}$ downward about 10% from its correct (unbiased) value according to eq. 12. Dynamic programming "recognized" that the equilibrium spawning stock

TABLE 1. Bayes equivalent and estimated optimum spawning stocks, in discrete levels, for a case where the Ricker model is assumed correct but the β (equilibrium stock) parameter is unknown. The rows represent $\sigma^2_{\hat{\beta}}$ increasing, from 0.0 to 0.02 by increments of 0.0022. The columns represent $\hat{\beta}$ increasing from 0.01 to 0.05; this roughly represents the equilibrium stock decreasing from 100 to 20.

	0.01			→		$\hat{\beta}$		→		0.05
					Bayes equivalent (no deliberate learning)					
0.0	45	31	26	21	19	14	13	12	12	11
↓	43	34	26	21	19	14	13	12	11	11
	37	31	25	21	18	14	13	12	11	11
	36	28	25	21	18	14	13	12	11	11
$\sigma^2_{\hat{\beta}}$	31	28	25	21	18	15	14	12	12	11
	28	25	21	21	18	15	14	12	12	12
	25	25	21	21	17	15	14	14	12	12
↓	25	21	21	21	17	16	15	14	14	12
	21	21	21	19	17	16	15	14	14	12
0.02	21	21	21	19	17	16	15	15	14	14
					Approximate optimal (at stage N−20)					
0.0	45	34	26	21	19	14	13	12	12	11
	43	34	26	21	19	14	13	12	11	11
↓	37	31	26	21	18	14	13	12	11	11
	36	31	25	21	18	14	13	12	11	11
	36	28	25	21	19	15	14	12	12	11
$\sigma^2_{\hat{\beta}}$	31	28	25	21	19	16	14	12	12	12
	31	25	25	21	21	17	15	14	12	12
↓	25	25	25	21	21	17	16	16	15	12
	25	25	21	21	19	18	17	17	14	14
0.02	25	25	21	21	19	19	19	16	15	16

TABLE 2. Apparent optimum policy for the β-unknown problem, computed with an accidental downward bias of around 10% in the $\hat{\beta}$ estimation. Compare to the approximate optimal policy in Table 1.

	0.01			→		$\hat{\beta}$		→		0.05
0.0	45	34	26	21	19	14	13	12	12	11
↓	43	34	27	21	21	14	13	12	12	11
	37	31	24	21	15	14	13	11	11	11
	33	33	24	21	15	14	12	11	11	11
$\sigma^2_{\hat{\beta}}$	35	26	21	18	15	15	12	10	9	10
	25	24	21	21	18	12	12	11	9	10
↓	24	24	24	17	15	15	12	9	9	8
	21	21	15	15	15	15	12	10	12	10
	18	18	18	18	15	13	13	11	10	10
0.02	18	18	17	17	14	12	13	11	11	11

was consistently overestimated, and called for lower spawning stocks.

Discussion

The numerical results presented above will be useful in designing heuristic policies for adaptive management, but they are not of immediate practical significance. They do not account for various constraints and complex objectives that exist in most real problems. They presume accurate systems for measuring recruitment and achieving desired escapements. It would rarely be credible to represent uncertainties through just two alternative hypotheses or variation in a single parameter. This section suggests how some of the difficulties can be addressed, and concludes with a general discussion about when it is worthwhile to employ actively adaptive policies.

COMPUTATIONAL LIMITS

With the largest of modern computers, a clever numerical analyst could now solve the adaptive control problem represented by the Ricker model with two unknown parameters (an 8-variable dynamic program). He would need to exploit fully various functional characteristics of the problem (for example $\hat{V}$ and $V^{\circ}(\cdot)$ can be approximated by polynomials), and would need several hours of CPU time. With advances in computing that are likely in the next decade or so, he might be able to

solve a problem with three or even four unknown parameters. But realistic models with many unknown parameters and more complex state representations (i.e. age structure) are likely to defy precise analysis for some time.

An alternative approach is to represent uncertainty by a collection of M alternative models, where M is large enough to cover the full range of outcomes that are considered credible. Wenk and Bar Shalom (1980) show that the optimum policy can then be found by solving $M(M-1)/2$ two-model problems. Two-model problems are reasonably tractable (the cases presented above required less than 1 min CPU time each) provided the system state is one- or two-dimensional.

It is often reasonable to represent the alternative hypotheses by piecewise linear relationships, as in Fig. 2. Then the computational requirements for each two-model case can be reduced considerably, since the optimum policy will usually be at one of a few well-defined points. A key need here is to develop simple approximations for the effect of learning on $\hat{V}$ and V^*.

Objectives, Constraints, and Risks

Adaptive management calls for variable escapements and recognizes that outomes are unpredictable. It can therefore conflict with management objectives, such as economic efficiency, that would be better served by providing stable and predictable catches. Most fisheries decisions represent outcomes of a bargaining process between users and institutional managers; the net effect of the process can be viewed most simply as constraints on policy change. There are two obvious ways to deal with these constraints. One is to attempt to eliminate them by imposing a storage system between the resource and its users; for example, catches (or revenues) from good years can often be stored (saved, invested) for use (or as income) in bad years. Optimum storage and release policies can then be found for each user (according to his own time preferences) as a rather trivial exercise in stochastic dynamic programming. The second, and analytically more difficult way is to include past decisions as part of the information state of the overall optimization problem. This adds at least one dimension (i.e. s_{t-1} or $R_{t-1} - s_{t-1}$) to the dynamic programming problem; a simple example is presented in Walters (1978). Other promising approaches for dealing with variability have been analyzed by Mendelssohn (1979, 1980).

Though we can devise policies for compromising between variability and stability, perhaps we should be more concerned with the long-term wisdom of providing stable harvests. Complex systems tend to simplify and become locked into vulnerable states when they do not receive variable inputs; they lose their "resilience" to respond to unexpected events (Holling 1973, 1978).

On various occasions the author has recommended to fisheries managers that more variable, informative, harvesting policies be employed. The usual reaction has been strongly risk averse, often expressed either as a high subjective probability on the more pessimistic model(s) or as a concern that some even more drastic outcome (depensatory mortality at low spawning stocks, "overspawning" at high stocks) may transpire. Whatever the argument, the basic aversion is to low catches in the immediate future. In part this may simply reflect high discount rates and desire to please (or prevent confrontation with) fishermen and dependent industries, who are justifiably shortsighted. However, it more often reflects a deplorable fear of making visible mistakes. Most managers are deliberately or implicitly charged with taking a longer view than their direct clients, and should therefore not be overly averse to short-term losses. Indeed, most fisheries operate on many areas and/or stocks, so there is opportunity for risk spreading; in such cases I see no compelling reason for managers not to act simply as expected value maximizers.

Measurement Errors

Measurement errors can have a profound effect on assessment of production and stock–recruit relationships (Uhler 1980; Mohn 1980; Walters and Ludwig 1981; Ludwig and Walters 1981a). Standard statistical procedures can give badly biased estimates, which for stock recruit cases will usually favor overexploitation. Bayes theorem can still be applied to provide the posterior distributions needed for adaptive management analysis, provided independent estimates are available for the measurement error variance. For example, suppose recruitment R_t is measured with a multiplicative, log-normal error, so the manager only sees $r_t = R_t e^{v_t}$ where v_t is normal with variance σ_v^2. Then equation (11) remains valid, but σ_w^2 is replaced by $\sigma_w^2 + \sigma_v^2$. The analysis becomes considerably more complicated when s_T is also measured with error.

Measurement errors have three general effects in adaptive formulations. First, they may increase the dimensionality of the information state needed to describe fully the Bayes posterior distribution at any time (parameter estimates and their covariances may not provide a complete set of sufficient statistics for the distribution). The lower dimensional analysis can still proceed in such cases, but the best policy becomes a function of the estimation procedure and will not be optimal in a general sense. Second, measurement errors make the Bayes distribution more uniform across possible models, so $\hat{s}_T$ remains suboptimal (with respect to the correct model) for longer than it would in the absence of measurement errors. This effect would tend to favor adaptive probing. Third, errors make each decision less informative about the correct model. This effect works against adaptive probing (makes probing less worthwhile). The balance between effects two and three is not clear and will likely depend on the specific problem being analyzed; probing will be favored in some cases, and will not be worthwhile in others.

When is Adaptive Probing Worthwhile?

Probing policies result in improved understanding of system responses, and it is disappointing from a scientific point of view to see how small an improvement they make in expected yield (0.2–0.5% per decision in the examples). The problems here are not that understanding has little practical value; rather, they are that (1) each probing decision has an implicit cost measured (in expectation) by lost yield if a more pessimistic hypothesis proves correct, and (2) the Bayes equivalent (passive adaptive) baseline policies usually result in considerable learning. Also, a small improvement per decision can result in large cumulative benefits if the discount rate is not too high.

It is difficult to construct a collection of hypotheses that imply different optimal policies and yields, but where the

pessimistic alternatives do not imply considerable losses for the manager who moves toward optima predicted by the optimistic alternatives. In part the problem results from trying to manage single systems as unique entities over time; when one system is assumed to be informative about others (other stocks, other cycle years in salmon, etc), the costs of disturbing it can be weighed against possible benefits across the whole collection. Also, informative variability can be introduced at lower net cost when there are several "replicate" systems, by alternately harvesting some replicates harder while backing off on others.

A critical step in adaptive policy design is the identification of alternative hypotheses that are consistent with historical experience yet reflect potential opportunities and dangers of altered escapements (or harvests). This step demands objectivity and imagination rather than analytical skill, and is not likely to be completely successful. The correct hypothesis may not become visible until some steps in its direction are taken. Nature contains a potentially infinite variety of surprises (opportunities and pitfalls). Even if the "right" model is found, it is not likely to remain so for long: the numbers that we call parameters are in fact complex functions of various biological and physical interactions, and are likely to be anything but constant over time. Some changes may reasonably be modelled as random environmental effects, but others are likely to be too persistent.

The manager who follows a "certainty equivalent" policy (assume best model is true, correct it as new observations become available) may stumble upon opportunities or accidently recognize changing parameters, but his actions will frequently be uninformative as well as incorrect (cf. Fig. 1, 2). His expected performance will improve considerably if he adopts a Bayes equivalent policy that at least recognizes untested opportunities and dangers. But the Bayes equivalent policy is not always informative (see second and third numerical examples), and additional benefit will usually result from some active probing in the direcion of recognized opportunities for higher yields.

From these remarks I draw a radical conclusion: regular probing actions should be a fundamental part of every fishery management plan. It is wrong to pretend that the answers are known, or that nature will reveal them before they are directly and deliberately experienced, or that once known they will remain correct for long. The goal of stock assessment should not be to devise the best possible production model; rather it should be to identify possible outcomes and policies for moving toward the more promising outcomes.

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Appendix

We seek to show when equations such as (5) and (8) are maximized by choosing a policy that accounts explicitly for the effect of current decisions on future uncertainty. The algebra is easiest to see for equation (8). The spawning stock that maximizes this equation is given by

$$(1a)\quad \frac{d\hat{V}_t}{ds_t} = 0 = -1 + \lambda \frac{d}{ds_t} \underset{\beta,w_T}{\mathcal{E}} V^*(R_{t+1}, \hat{\beta}_{t+1}, \sigma^2_{\hat{\beta}t+1}, \beta).$$

Let us denote the expectation with respect to β and w_t simply as $\hat{V}_{t+1}$. R_{t+1} depends explicitly on s_t, as do $\hat{\beta}_{t+1}$ and $\sigma^2_{\hat{\beta}_{t+1}}$ (see eq. (12)). Differentiating it with respect to s_t, we get

$$(2a)\quad \frac{d\hat{V}_{t+1}}{ds_t} = \underset{\beta,w}{\mathcal{E}} \frac{\partial \hat{V}_{t+1}}{\partial R_{t+1}} \frac{dR_{t+1}}{ds_t} + \underset{\beta,w}{\mathcal{E}} \left(\frac{\partial V^*(\cdot)}{\partial \hat{\beta}_{t+1}} \cdot \frac{d\hat{\beta}_{t+1}}{ds_t} + \frac{\partial V^*(\cdot)}{\partial \sigma^2_{\hat{\beta}_{t+1}}} \cdot \frac{d\sigma^2_{\hat{\beta}_{t+1}}}{ds_t} \right).$$

The product containing $\hat{\beta}$ in (2a) represents the dependence of $\hat{\beta}_{t+1}$ on s_t; its expected value with respect to β and w is zero under the conditions for which equation (12) is valid (w and β normally distributed). The expectation therefore simplifies to the product containing $\sigma^2_{\hat{\beta}_{t+1}}$.

Substituting the simplified (2a) into (1a) and rearranging terms, we get that the optimum spawning stock satisfies

$$\underset{\beta,w}{\mathcal{E}} \frac{\partial \hat{V}_{t+1}}{\partial R_{t+1}} \frac{dR_{t+1}}{ds_t} = \frac{1}{\lambda} - \underset{\beta,w}{\mathcal{E}} \frac{\partial V^*(\cdot)}{\partial \sigma^2_{\hat{\beta}_{t+1}}} \frac{d\sigma^2_{\hat{\beta}_{t+1}}}{ds_t}$$

If the Bayes equivalent policy is computed by ignoring $\sigma^2_{\hat{\beta}_{t+1}}$, or by assuming that it is independent of s_t, then it will simply satisfy $\underset{\beta,w}{\mathcal{E}} \frac{\partial \hat{V}_{T+1}}{\partial R_{t+1}} \cdot \frac{dR_{t+1}}{ds_t} = \frac{1}{\lambda}$. If the expectation in (3a) is greater than zero, and if $\hat{V}_{t+1}$ is a dome-shaped function of s_t (it generally is for stock-recruitment models), then the optimum s_t will be larger than the Bayes equivalent s_t.

By equation (12), $d\sigma^2_{\hat{\beta}_{t+1}}/ds_t \leq 0$, and is equal to 0 only if $s_t = 0$ or $\sigma^2_{\hat{\beta}_t} = 0$. Therefore $\sigma^2_{\hat{\beta}_t} = 0$ is one (trivial) condition under which the Bayes equivalent policy is optimal. The interest then centers on $\partial V^*(\cdot)/\partial \sigma^2_{\hat{\beta}_{t+1}}$, which measures the sensitivity of future returns to uncertainty about β. But this term can be greater than zero only if increased uncertainty at time $t+1$ leads to an improved decision $\hat{s}_{t+1}$ (on average across possible true β's), and will equal zero if $\hat{s}_{t+1}$ is independent of $\sigma^2_{\hat{\beta}_{t+1}}$. $\hat{s}_{t+1}$ can be independent of $\sigma^2_{\hat{\beta}_{t+1}}$ (i.e. if $V^*_{t+1}(\cdot)$ is linear in β), but in such cases it is unnecessary to compute even the Bayes equivalent policy. Curiously, it is possible for increased $\sigma^2_{\hat{\beta}_{t+1}}$ to result in improved decisions, if for example $\hat{\beta}_{t+1}$ can only be estimated by some biased procedure that converges to an incorrect estimate of β as $\sigma^2_{\hat{\beta}_{t+1}}$ approaches zero but will move toward the actual β provided that $\sigma^2_{\hat{\beta}_{t+1}}$ remains large. However, in general we expect that $\partial V^*_{T+1}(\cdot)/\partial \sigma^2_{\hat{\beta}_{t+1}}$ will be less than zero, since increasing $\sigma^2_{\hat{\beta}_{t+1}}$ will result in the decision $\hat{s}_{t+1}$ being "weighted" more by incorrect values of β (i.e. moving farther from whatever s^* is truly optimal). This argument also helps to see why the optimal $\hat{s}_{t+1}$ has an expected value only slightly different from the Bayes equivalent decision: in expectation the difference $\hat{s}_t - s^*$ will not be changed very much by the reduction in $\sigma^2_{\hat{\beta}_{t+1}}$ implied by any single "informative" decision s_t.

Adaptive Management of Stock–Recruitment Systems

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SMITH, A. D. M., and C. J. WALTERS. 1981. Adaptive management of stock–recruitment systems. Can. J. Fish. Aquat. Sci. 38: 690–703.

Management of escapements can be formulated as a problem in stochastic optimal control. Using the Ricker model as a reasonable representation of the average stock–recruit relationship, approximate optimal policies are found for cases where there is parameter uncertainty as well as environmental variation, by employing a "wide-sense adaptive dual control" algorithm. This algorithm accounts for the future information value of any escapement choice as well as the effect on immediate yield. The algorithm indicates that escapements should be deliberately varied to obtain better information for future management, provided that historical escapement levels have not been extremely variable. Such actively adaptive, or probing policies will become progressively more important in the future as managers learn how to control escapements more precisely and thus eliminate natural sources of informative variation.

Key words: adaptive management, stock–recruitment, escapement

SMITH, A. D. M., and C. J. WALTERS. 1981. Adaptive management of stock–recruitment systems. Can. J. Fish. Aquat. Sci. 38: 690–703.

La gestion des poissons échappant à la capture peut être formulée comme un problème de contrôle optimal stochastique. Le modèle de Ricker nous donnant une représentation raisonnable de la relation stock–recrutement moyenne, on peut utiliser un algorithme de « double gestion adaptive au sens large » (*wide sense adaptive dual control*) pour en arriver à des politiques d'approche optimales dans les cas où il y a incertitude dans les paramètres ainsi que variation dans l'environnement. Cet algorithme tient compte de la valeur de l'information future sur tout choix d'evitement de même que l'effet sur le rendement immédiat. L'algorithme indique que le nombre de poissons qui échappent à la capture devrait être délibérment changé afin d'obtenir une meilleure information pour la gestion future, pourvu que les niveaux historiques d'échappement n'accusent pas de variations extrêmes. De telles politiques activement adaptives ou d'expérimentation prendront de plus en plus d'importance, à mesure que les gestionnaires apprendront à régler plus précisément le nombre de poissons qui s'échappent, éliminant de cette façon les sources naturelles de variation de l'information.

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MUCH of our understanding of fish stock dynamics has come from information generated by the process of harvesting the stocks. Information such as catch and effort, observations of escapement and recruitment, and in some cases the qualitative composition of the catch are used to estimate the parameters of simple models of stock dynamics. Such models are then used as a basis for managing the stocks, given some objective such as maximum sustainable yield.

Given a historical set of data and a model which is assumed to describe adequately the dynamics of the stock, three different strategies for the subsequent management of the fishery can be identified. First, historical data can be used to estimate the parameters of the model, and the fishery can then be managed into the future while assuming that these initial estimates represent the true parameters of the stock. Second, the initial parameter estimates can be used at first, but the estimates can be updated from time to time as new data become available from the fishery. At any given time the current parameter estimates are assumed to be correct. Third, the fishery can be managed so as to generate data deliberately, which will subsequently improve parameter estimates. For example, the stock might be deliberately overfished (according to current parameter estimates) to test whether it might

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not, in fact, be more productive at lower stock sizes.

The term adaptive management has been used in the fishery literature (Walters and Hilborn 1976, 1978; Silvert 1978) to describe situations in which learning takes place as management proceeds. The three types of strategies outlined above can be described as nonadaptive, passively adaptive, and actively adaptive, respectively. In the control theory literature, they are sometimes called open-loop, open-loop feedback, and closed loop. The first involves no further learning after a certain time, the second involves accidental learning as time proceeds, and the third involves a deliberate attempt to promote learning. Most management practice probably lies somewhere between the frist two strategies, with occasional updating of data sets and revision of parameter estimates. The active adaptive strategy has rarely been used, although experimental management programs have been undertaken for halibut (Skud 1973) and tuna (IATTC 1977).

Theoretical interest in adaptive management, or more generally in the problems posed by uncertainty in managing renewable resources, is of very recent origin. Walters and Hilborn (1976) and Walters (1981) used stochastic dynamic programming to determine optimal control laws accounting for statistical uncertainty in parameter estimates of the Ricker stock–recruitment model. They considered cases of uncertainty in one parameter at a time and did not test the control laws generated. Walters (1977) proposed techniques for evaluating possible benefits of experimental policies for enhancement of Pacific salmon. Silvert (1978) applied the concepts of active and passive adaptive control to the problem of choosing between two alternative model forms, and showed that optimal decisions were very sensitive to discount rates. Ludwig and Walters (1981) developed methods for calculating control policies which average over statistical uncertainty in parameter estimates. Mendelssohn (1979) used a similar approach. Walters and Hilborn (1978) reviewed the theory and applications in the broader field of ecological management.

This paper develops a range of adaptive policies for managing fish stocks with uncertain dynamics. In particular, some recent advances in stochastic optimal control theory (Bar-Shalom and Tse 1976) are used to develop an actively adaptive control policy which takes deliberate account of uncertainty in managing dynamic systems. A brief outline of the theory involved is included in the Appendix, for those readers who may wish to explore further in the control theory literature.

The adaptive policies are applied to the management of simulated stocks where the major source of uncertainty is in the form of the stock–recruitment relationship. This is the case for many salmon fisheries. The Ricker model (Ricker 1954) is assumed to describe the relationship adequately and uncertainty is represented as statistical uncertainty in the parameter estimates of this model. Considering each set of parameter estimates as a hypothesis about the form of the stock–recruitment relationship, statistical uncertainty in parameter estimates can be thought of simply as inability to distinguish between a number of alternative hypotheses about the dynamics of the stock. Our aim is to compare the performance of the various adaptive policies in maximizing long-term yield, faced with uncertainty about stock–recruitment dynamics.

Parameter Estimation for the Ricker Model

Ricker's model can be expressed as:

$$(1)\quad R_{t+1} = S_t \exp\{\alpha - \beta S_t + v_{t+1}\}$$

where R_{t+1} is recruitment in generation $t+1$ produced by escapement S_t in generation t. Alpha (α) and beta (β) are parameters of the model, and v_{t+1} is an environmental "noise" term, normally distributed with zero mean and variance σ_v^2. Walters and Hilborn (1976) justify the assumption that v is normally distributed and R. M. Peterman (unpublished data) presents empirical evidence that v is normal for several salmon stocks.

Observations of recruitment are assumed to be available, with the observation being:

$$(2)\quad R_t^{\text{obs}} = R_t \exp\{w_t\}$$

where w_t is the observation or measurement error, and is assumed to be normally distributed with zero mean and variance σ_w^2. It will be assumed here that S_t is measured without error; the dangers of this assumption have been pointed out by Walters and Ludwig (1981) and Ludwig and Walters (1981).

Combining (1) and (2):

$$R_{t+1}^{\text{obs}} = S_t \exp\{\alpha - \beta S_t + v_{t+1} + w_{t+1}\}$$

which can be rewritten

$$(3)\quad \ln[R_{t+1}^{\text{obs}}/S_t] = \alpha - \beta S_t + v_{t+1} + w_{t+1}$$

which is a linear regression of the form

$$y = \alpha + \beta x + e$$

where $y = \ln[R_{t+1}^{\text{obs}}/S_t]$ and $x = -S_t$. With the assumptions that have been made about the noise processes, the error term e in the regression is normally distributed with zero mean and variance $\sigma_e^2 = \sigma_v^2 + \sigma_w^2$.

Dahlberg (1973) has shown how parameter estimates of the Ricker model can be obtained from this formulation, and Walters and Hilborn (1976) have shown how recursive parameter estimation algorithms can be used to obtain both the parameter estimates, and the associated parameter error covariance matrix

$$P_t = \begin{bmatrix} \hat{\sigma}_\alpha^2 & \hat{\sigma}_{\alpha\beta} \\ \hat{\sigma}_{\alpha\beta} & \hat{\sigma}_\beta^2 \end{bmatrix}$$

which measures the uncertainty about the parameter estimates given data up to time t. The elements of $\hat{P}_t$ define a region of uncertainty around the mean estimate $[\hat{\alpha}\ \hat{\beta}]$.

The elements of $\hat{P}_t$ are completely determined by four statistics of the available data set: the mean escapement $\bar{S}$, the variance in past escapements S_s^2, the number of data points t, and the variance σ_e^2 about the regression. Using these quantities, intuitively meaningful expressions for $\hat{P}_t$ become

$$\hat{\sigma}_\alpha^2 = \left[\frac{1}{t} + \frac{\bar{S}^2}{(t-1)S_s^2}\right] \cdot \hat{\sigma}_e^2$$

$$(4) \quad \hat{\sigma}_{\alpha\beta} = \left[\frac{\bar{S}}{(t-1)S_s^2}\right] \cdot \hat{\sigma}_e^2$$

$$\hat{\sigma}_\beta^2 = \left[\frac{1}{(t-1)S_s^2}\right] \cdot \hat{\sigma}_e^2.$$

Uncertainty in the α parameter will be lowest when the mean of past escapements is low, since α is the intercept of the regression at zero escapement. Since $-\beta$ is the slope of the regression, the uncertainty in the β parameter does not depend on the mean escapement but is reduced as the variance of past escapements increases. As expected, uncertainty decreases as the number of data points increases and as the regression error variance (equivalent to variance in environmental and observational noise) decreases.

Range of Control Policies Tested

The range of policies to be applied to the management of the simulated salmon stock includes the following:

1) The optimal policy (OP) where the true parameters of the stock are known. The performance of this policy serves as an upper bound on the performance of any policy which might be tested.

2) An active adaptive policy (AAP) based on the wide sense-adaptive dual control algorithm described in the Appendix. The escapement chosen at each stage is a function both of the parameter estimates and of the uncertainty in those estimates, as measured by the error covariance matrix.

3) Various passive adaptive policies (PAP). These have the property that the escapement chosen at any stage is a function only of the available parameter estimates, and assume that the estimates available at any time represent the true parameters of the stock and that the stochastic variation v_t can be ignored. These policies all make use of information which becomes available as management proceeds, but differ in how available data are used to update parameter estimates. Specifically, they differ by:

a) the number of data points which are allowed to accumulate between parameter estimate updates; and

b) the extent to which each new data point on the stock–recruitment relationship is given its due weight in revising the parameter estimates. This is varied by introducing a multiplicative factor GF ($0 < GF \leq 1$) to the estimation filter gain. The lower the value of GF, the less weight is given to each new data point.

In what follows, unless otherwise stated, a passive adaptive policy will refer to a policy which updates parameter estimates at each stage giving full weight to the new information.

4) A nonadaptive policy (NAP). This makes no use of real-time information and chooses the same escapement each year based on the initial parameter estimates. (Note that this policy is equivalent to the passive adaptive policy with $GF = 0$ or with the number of years between parameter estimate updates being infinite.)

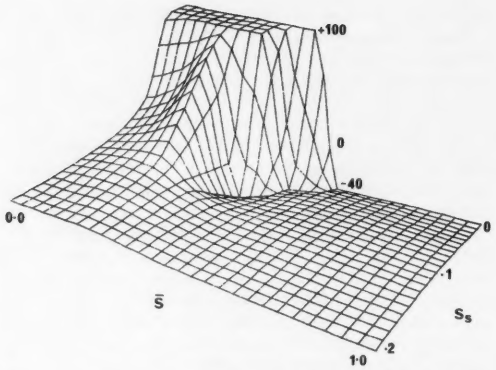

FIG. 1. Active adaptive control law: effect of mean $\bar{S}$ and standard deviation S_s in prior escapements. The height of the graph for any combination of $\bar{S}$ and S_s represents the percentage of increase or decrease in escapement chosen by the active adaptive policy relative to that which would be chosen by the passive adaptive policy. Nominal case: 10 yr initial data; $\alpha = 2.0$; discount rate = 0%; $\sigma_v^2 = 0.04$; $\sigma_w^2 = 0.04$.

Active Adaptive Control Law

Although it is not possible to obtain the control law for all possible combinations of parameter estimates and covariance matrices, it is of interest to determine the nature of the active adaptive control for a subset of possible combinations. In particular, we would like to know how the control should change in relation to the uncertainty in the parameter estimates. It was shown (eq. 4) that this uncertainty is measured by the mean escapement $\bar{S}$, the variance in the escapement S_s, the number of data points t, and the regression error variance $\sigma_e^2 = \sigma_v^2 + \sigma_w^2$. This section will show how the control action should change in relation to these four statistics. The effect of stock productivity and discounting of catches will also be explored.

Several sets of stock–recruitment data were generated by simulation, each set being specified by the mean and variance of the escapement and by the number of data points. The same random set of environmental and observational noise values (v_t, w_t) was used for each set. Parameter values and noise variances were based on actual data for Skeena River sockeye salmon (F. Wong, Institute of Animal Resource Ecology, U.B.C., personal communication).

From these data sets, parameter estimates and error covariance matrices were obtained. These could not be used directly in the dual control algorithm, since this requires state estimates and covariance matrices (see Appendix). However, because of the Ricker model being linear in the parameters, the transformation of distributions is straightforward.

From the state estimate and error covariance obtained in this way, the active adaptive control action can be calculated. The resulting control law is shown in Fig. 1 as the percentage

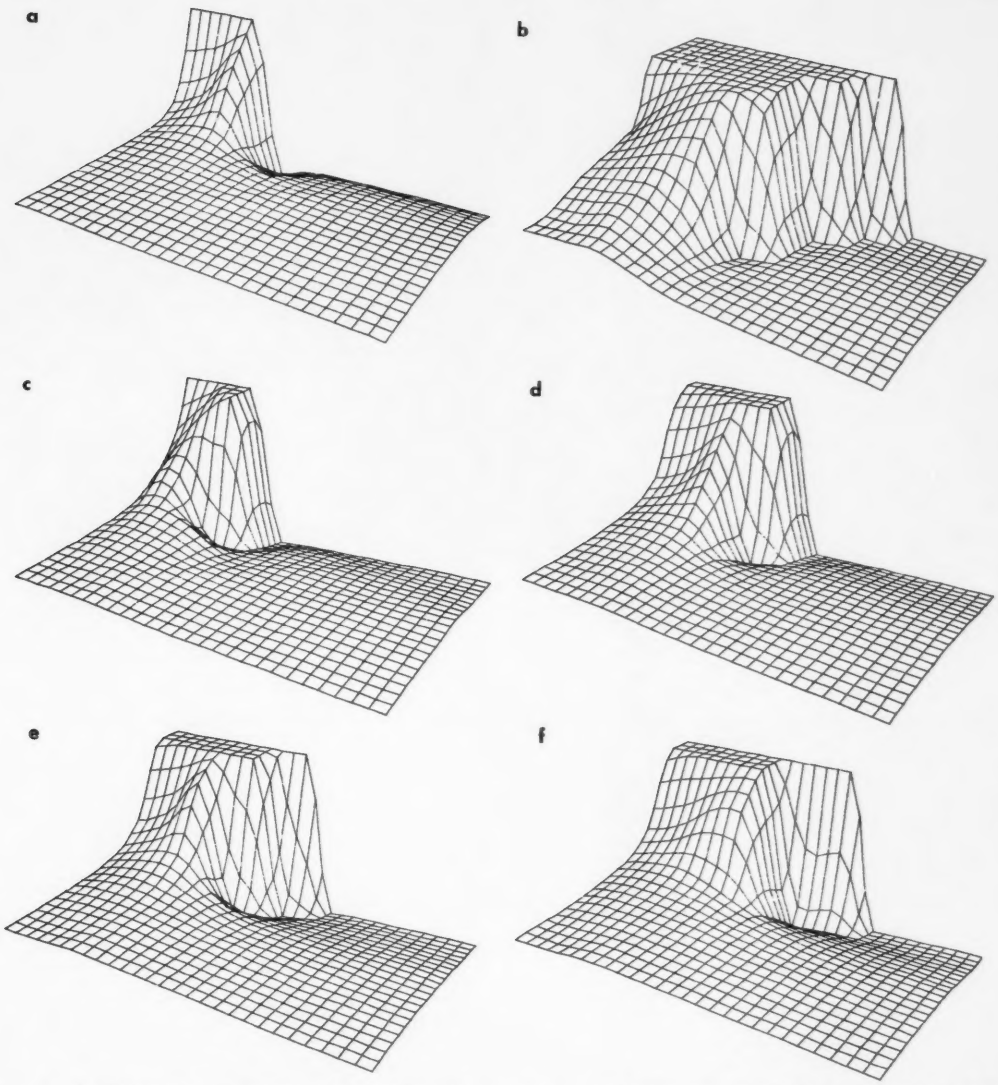

FIG. 2. Control laws as in Fig. 1 but with (a) 20 yr initial data; (b) $\alpha = 1.0$; (c) $\alpha = 3.0$; (d) discount rate = 10%; (e) $\sigma_w^2 = 0.16$; (f) $\sigma_w^2 = 0.36$.

of increase or decrease in escapement chosen by the active adaptive policy relative to that which would be chosen by the passive adaptive policy for the same parameter estimates.

The results for this nominal case seem intuitively reasonable. If the mean escapement has been low and the variance in escapement small, the best action is to allow a high, "probing" escapement. If the mean escapement has been high, a low escapement should be chosen. At intermediate levels of past escapement, either a very high or very low escapement should be chosen. In all cases where the variability in escapement has been low, the optimum is well outside the range of previously observed escapements. As variability in past escapements increases, the amount of probing by the active adaptive policy can be seen to decrease.

The effect of increasing the number of data points from 10 to 20 is shown in Fig. 2a. This reduces initial uncertainty about the parameters; the control law responds by reducing the perturbation to escapement. However, the perturbation is

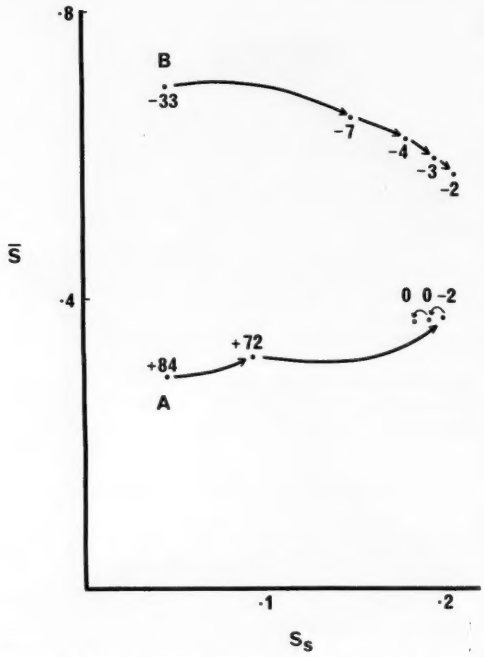

FIG. 3. Active adaptive trajectories and their affect on the mean $\bar{S}$ and variability S_s in escapement. Numbers beside points on trajectories represent percentage of increase or decrease in escapement chosen by the active adaptive policy relative to that which would be chosen by the passive adaptive policy.

still substantial if the initial variability in escapement is low.

The effect of the apparent productivity of the stock is shown in Fig. 2b and c. In both cases the covariance matrices are the same as in the nominal case, but the estimates of the α parameter (the stock productivity) are lower and higher, respectively. The ratio $\hat{\alpha}/\hat{\beta}$ of the parameter estimates is the same as in the nominal case, so the equilibrium stock sizes are the same. The results indicate that if the stock is thought to be of low productivity, then the response of the stock at high levels of escapement should be explored, unless the mean escapement has been very high relative to the estimated equilibrium stock size. On the other hand if the productivity is apparently high the best strategy is to try to improve the estimate of this productivity.

The effect of the discount rate is shown in Fig. 2d. The form of the control law in relation to the mean variance of the past escapements is not very different from the nominal case where the discount rate is zero. The extent to which the escapement is perturbed from the passive adaptive control is reduced slightly, and there is some indication that the control is less willing to explore in the direction of higher escapements.

The effect of the observation noise variance is shown in Fig. 2e and f. The sensitivity of the control to this level is important to determine, since it is assumed that the probability distributions of the noise processes are known, when in fact they must be estimated and may be in error. The form of the control law seems to be relatively insensitive to variations in the assumed noise variance. Since environmental and observational noise are indistinguishable in the stock–recruitment relationship, the control should also be insensitive to assumptions about the environmental noise variance. It should not matter how the overall variance is partitioned between the two sources.

Before proceeding to an evaluation of the performance of the three types of policies, it is of interest to note how the active adaptive policy results in a trajectory through ($\bar{S}$, S_s) space. Two such trajectories are shown in Fig. 3 starting from the same initial variability in escapement at two different levels of mean escapement. At each point "sampled" by the active adaptive policy, the percentage of increase or decrease in escapement relative to the passive adaptive escapement is plotted.

For trajectory A, starting from low mean prior escapement, the initial control choise is to increase the escapement resulting in a slight increase in $\bar{S}$ but a substantial increase in S_s. The subsequent increase in escapement causes another increase in $\bar{S}$ and S_s, bringing the trajectory into the region where decreases in escapement are chosen. However, by this time the variability in escapement is great enough that only small perturbations are indicated and the active adaptive policy essentially becomes passive.

For case B, where the mean prior escapement has been higher, the trend is towards decreasing $\bar{S}$ and increasing S_s. In this case the decrease in $\bar{S}$ is not rapid enough to enter a region where the direction of perturbation is reversed before the variability in escapement has increased to an extent where further perturbations are not considered worthwhile.

Method of Policy Evaluation

The aim is to compare policies, based on a range of adaptive strategies, for their effectiveness in managing a resource with uncertain dynamics. In this case the resource is a simulated stock whose underlying dynamics are determined by the Ricker stock–recruitment equation. Uncertainty arises because of environmental and observational noise. Managing the stock involves choosing an escapement at each stage with the overall goal of maximizing long-term discounted yield.

The method for evaluation of policy performance involves the specification of an initial distribution of parameter estimates, that is, initial estimates $\hat{\alpha}$ and $\hat{\beta}$ and error covariance matrix $\hat{P}$. From this initial distribution of the estimates, actual parameter values are chosen at random which then become the true parameter values of the Ricker model for a particular simulation. From these initial conditions, and using the same set of random environmental and observational noise perturbations, each policy is applied to the management of the "stock," and the fishery is simulated over a number of years. Where appropriate to the policy, parameter estimates are updated using a recursive least squares estimator (Walters and Hilborn 1976).

Two performance measures are obtained for each policy for each simulation. The first measure, PM_S, is the sum of the

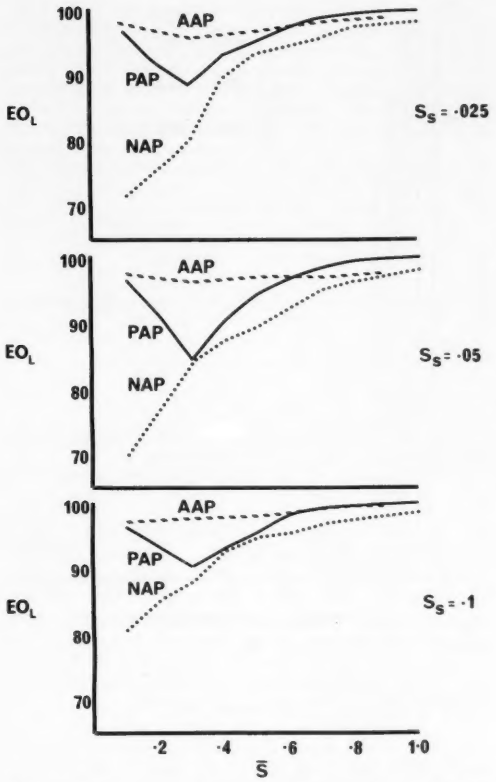

FIG. 4. Comparison of the expected performance EO_L of the three adaptive policies relative to the optimal performance, expressed as a percentage. The effect of mean $\bar{S}$ and standard deviation S_S in prior escapements is shown.

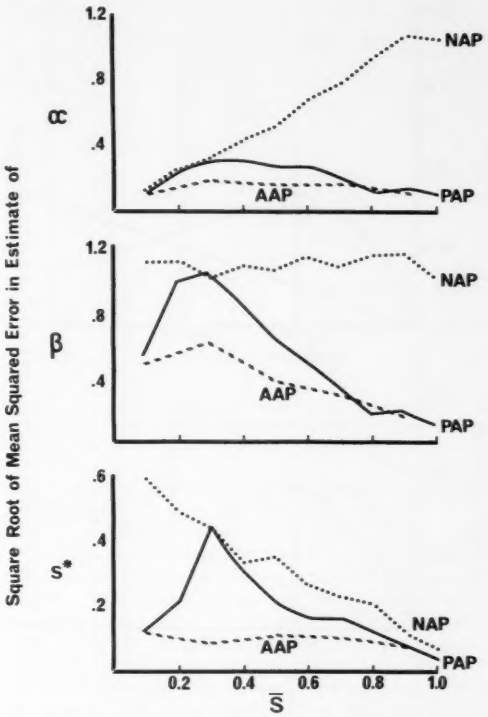

FIG. 5. Comparison of the performance of the three adaptive policies in estimating the parameters α and β of the Ricker model, and in estimating the optimal escapement S^*.

discounted catches over 20 generations of the stock, plus the discounted final stock size. The second measure, PM_L, is the sum of the discounted catches over the 20 generations plus the expected future value of the catch which would be obtained after the final year of simulation. This expected future value of catch is calculated by assuming that the parameter estimates obtained by the end of the simulation period are used to determine the control policy from that time on with no further learning (i.e. a nonadaptive policy after the 20th generation). Where the discount rate is zero, a time horizon of 50 generations is set. The values for PM_S and PM_L can be considered as measures of the short-term and long-term performance of a particular policy.

Relative measures of the performance of each of the adaptive policies were obtained by expressing PM_S and PM_L as a percentage of the corresponding values for the optimal policy with known parameters. These relative measures are denoted PO_S and PO_L.

The expected value of a policy for a particular initial distribution of parameter estimates was obtained by simulating a large number of times, each time choosing the true parameter values for the simulation at random from the prior distribution of the estimates. Fifty simulations were deemed sufficient to determine the expected value. The expected values for a policy are denoted EV_S and EV_L and the expected values as a percentage of the expected value of the optimal policy are denoted EO_S and EO_L.

Policy Comparisons

The relative performances of the three basic types of adaptive policy — active adaptive, passive adaptive, and nonadaptive — were compared across a range of distributions of initial parameter estimates. The range of distributions tested was determed by the mean and variance of the escapement in the data available before beginning implementation of each policy.

The major result for policy analysis of the Ricker model is summarized in Fig. 4 which shows the relative expected long-term performance EO_L of the three policies across a range of mean prior escapements and for three different levels of prior variability in escapement. The mean of the prior escapements $\bar{S}$ has a large effect on the relative performances of the three policies. In each case, the performance of the non-

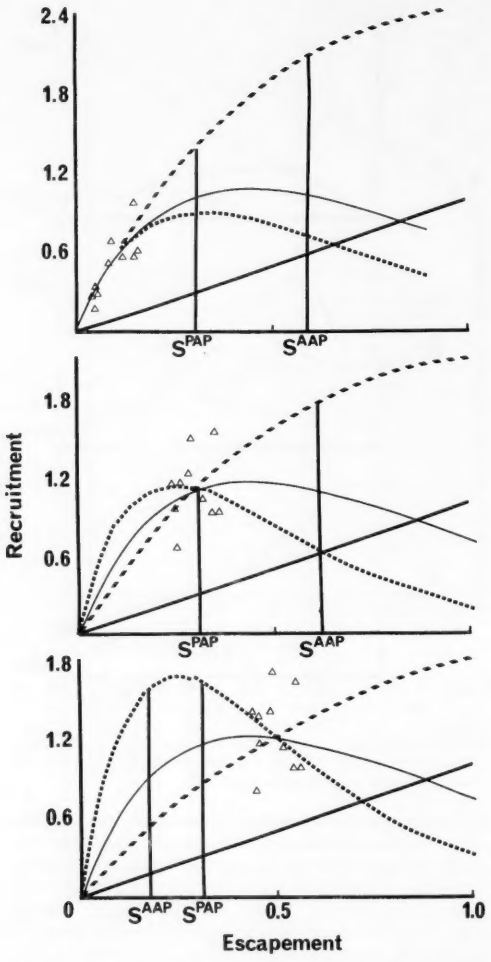

FIG. 6. Escapements chosen in relation to prior stock–recruitment data (shown as triangles). The solid curve through each set of data is the line of best fit. The two broken lines represent alternative lines of good fit. Vertical bars show the levels of escapement chosen by the active and passive adaptive policies on the basis of the data.

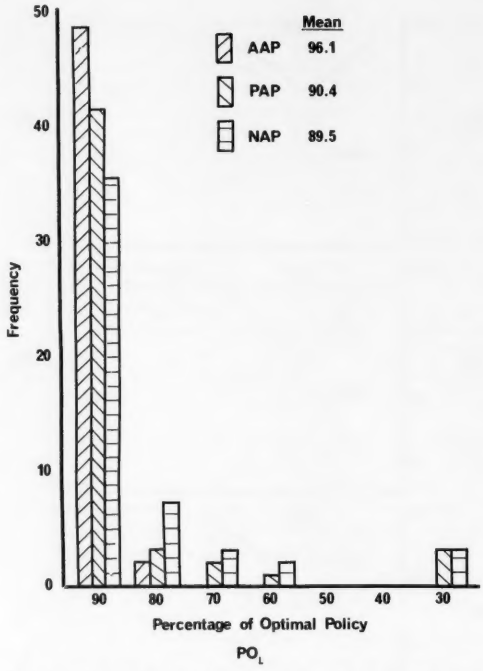

FIG. 7. The distribution of relative policy performances PO_L over the 50 simulations for the case $\bar{S} = 0.3$; $S_v = 0.05$.

adaptive policy improves steadily as $\bar{S}$ increases. The passive adaptive policy performs very well for low and high prior escapements, but poorly for medium levels of $\bar{S}$. The active adaptive policy does well in all cases.

The estimation performances of the three policies, as measured by the square root of the mean squared error in the estimates of the α and β parameters as well as in the estimate of the optimum escapement S^*, are shown in Fig. 5. The errors in the estimates are measured at the end of each 20-generation simulation, and the mean is over the 50 simulations for each prior data set.

Both the active and passive adaptive policies estimate the α parameter quite well, though the passive adaptive estimation is worst at medium levels of prior escapement. The increasing error in the α estimate with the nonadaptive policy simply reflects the effects of $\bar{S}$ on σ_α^2 in equation (4).

The error in the estimate of the β parameter for the nonadaptive policy is independent of the mean prior escapement as predicted by equation (4). The poor estimates of the β parameter at medium levels of prior escapement with the passive adaptive policy accounts for its poor estimate of S^* at that level, which in turn accounts for its poor performance. The performance of each policy corresponds closely to the estimation performance in determing S^*, as it should do.

The explanation of the results summarized in Fig. 4 and 5 is straightforward. The improved performance of the nonadaptive policy as the mean escapement increases is due to a combination of two factors. First, the estimate of the equilibrium stock size α/β improves as the mean escapement increases, and second, the optimum escapement S^* is relatively insensitive to the particular levels of α and β provided their ratio α/β is known. Estimates of both α and β are very poor for the nonadaptive policy at high mean escapement, yet the estimate of S^* and the resulting performance are good.

The passive adaptive policy performs well for both low and high prior escapements because in these cases its deterministic policy chooses escapements well outside the range of observed prior escapements. Only when the deterministic es-

TABLE 1. Comparison of short-term and long-term performance. (a) Mean performance as a percentage of mean performance of the optimal policy; (b) percentage improvement of policy x over policy y relative to the mean performance of policy y; (c) number of simulations (out of 50) for which the relative long-term performance exceeds the relative short-term performance. * Denotes significant effect (at 5% significant level). Results shown in parentheses are for the case where the discount rate is 5%.

a)	AAP	PAP	NAP
20 yr	94.4	84.7	84.2
	(92.9)	(85.1)	(84.9)
50 yr	96.2	84.5	83.7
	(94.6)	(84.7)	(84.3)

b)	AAP vs. PAP	PAP vs. NAP
20 yr	11.4	0.6
	(9.3)	(0.2)
50 yr	13.8	1.0
	(11.7)	(0.4)

c)	AAP	PAP	NAP
	48*	28	21

capement falls within the range of the prior escapements will this "self generating" perturbation by the passive adaptive policy fail to operate.

This point is exemplified in Fig. 6 which shows the stock–recruitment data for three cases of increasing mean prior escapement. The solid lines through the data represent the best fit of the Ricker model and the broken lines represent alternative possible forms of the model which fit the data almost equally well. The escapement S^{PAP} chosen by the passive adaptive policy based on the best estimate is plotted in each case. It is evident that only in the case $\bar{S} = 0.3$ does this escapement fall within the prior range of escapements. The escapements chosen in the other two cases stand a good chance of discriminating between the alternative model forms.

The escapment S^{AAP} which would be chosen by the active adaptive policy is also plotted in Fig. 6. This policy always chooses escapements outside the prior observed range and at a level which would effectively discriminate between the alternative model forms (representing different parameter estimates). This property of the active adaptive policy accounts for its high level of performance across the entire range of mean prior escapements.

It is perhaps surprising that even the nonadaptive policy achieves, at worst, no less than 70% of the optimal performance. This is because the true parameter values, chosen at random from the initial distribution of estimates, only rarely fall at the extremes of that distribution, far from the mean values on which the nonadaptive policy bases its choices of escapement.

POLICY COMPARISON: CASE $\bar{S} = 0.3$, $S_S = 0.05$

The greatest difference in performance between the active and passive adaptive policies occurs where the initial passive adaptive escapement chosen falls within the range of the escapements already observed. This section will examine more closely the results of individual simulations for the case $\bar{S} = 0.3$, $S_S = 0.05$, where this effect has occurred.

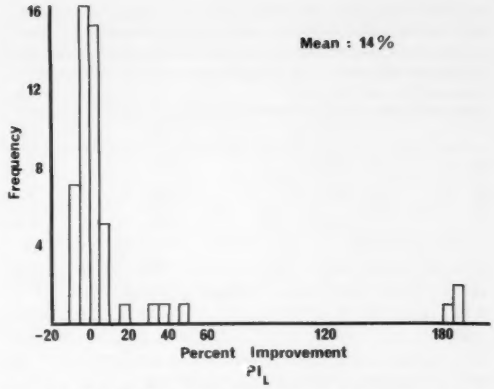

FIG. 8. The distribution of the percentage of improvement of the active adaptive policy relative to the passive adaptive policy over the 50 simulations for the case $\bar{S} = 0.3$; $S_S = 0.05$.

The first point to note is that the active adaptive policy always performs well relative to the optimal policy where the true parameters are known. The frequency distribution of the long-term performance PO_L of each policy relative to the optimal is shown in Fig. 7. The mean performace of each policy is high, but the active adaptive policy always performs well (80% of the optimal or better) whereas the other two policies occasionallly perform very poorly (as low as 30% of the optimal policy) though this does not happen very frequently.

The next point to note is that although the active adaptive policy does well in the long term, it does so at the expense of short-term performance (Table 1). The active adaptive policy must sacrifice short-term payoff (catch) to improve the parameter estimates and so do better in the long term. The passive adaptive and nonadaptive policies do equally well (or poorly) in the short term and the long term. The other indication that the active adaptive policy sacrifices short-term performance is that the introduction of a discounting rate of 5% reduces the performance relative to the optimal performance.

The next item of interest is the improvement in performance of the active adaptive policy over the passive adaptive policy in individual cases. The quantities of interest, PI_S and PI_L, represent the short-term and long-term percentage improvement in performance of the active adaptive policy over the passive adaptive policy relative to the performance of the passive adaptive policy. The frequency distribution of PI_L over the 50 simulations is shown in Fig. 8. The mode of the distribution is near zero, that is, in most cases the performance of the two policies is very similar. However, the distribution is also skewed. Negative values are of small magnitude but positive values are occasionally quite large. This means that the active adaptive policy never performs much worse than the passive adaptive policy, and occasionally it performs very much better.

The average improvement of 14% is not significantly different from zero over the 50 simulations. Referring to Fig. 7,

TABLE 2. Comparison of estimation performances. Shown in the table are the square root of the mean squared errors in the estimates of the two parameters and the optimum escapement S^*. * Denotes a significant difference (at 5% significant level) in estimation performance between policies.

	AAP	PAP	NAP
α	0.19*	0.32	0.33
β	0.63*	1.05	1.03
S^*	0.08*	0.43	0.43

even the nonadaptive policy achieves 90% of the optimal performance in most cases. Comparing the performance of the active and passive adaptive policies over the simulations where the performance of the nonadaptive policy is less than 90% of the optimal, the improvement in performance of the active adaptive policy is highly significant.

The estimation performance of the three policies is presented in Table 2. The estimation performance for the active adaptive policy is significantly better than that for the passive adaptive policy, which does no better than the nonadaptive policy.

The effect of the active adaptive policy in reducing parameter uncertainty and hence improving long-term performance can be seen in the detailed analysis of a particular simulation. Figure 9 shows the sequence of escapements chosen by the active and passive adaptive policies, together with the resulting parameter estimates and uncertainties. The initial estimation error is quite large, but rapidly improves with the active adaptive policy. The parameter estimates for the passive adaptive policy change little over time, and show no sign of approaching the correct values.

Figure 10 shows the stock–recruitment data generated by the active and passive adaptive policies together with the prior data. The solid line represents the true stock–recruitment relationship and the broken lines represent the estimated stock–recruitment relationships after management for 10 generations. These lines correspond closely for the active adaptive policy because the data points span a wide range of escapement levels. However, the escapements chosen by the passive adaptive policy all lie within the range of the prior escapements and the correct form of the relationship is never learned.

The cumulative discounted catch over time for the active adaptive, passive adaptive, and optimal policies is compared in Fig. 11. Although the active adaptive policy very quickly learns the correct parameter values, it performs very poorly over the first few stages and does not surpass the passive adaptive policy until the sixth generation. However, by the 20th generation its performance compares very favorably with the optimal policy, whereas the passive adaptive policy has fallen well behind. After 50 generations the improvement in performance of the active adaptive policy over the passive adaptive policy is 45%.

POLICY COMPARISON: CASE $\bar{S} = 0.1$, $S_S = 0.05$

This case represents the situation in which there is the greatest difference in performance between the passive adaptive and nonadaptive policies. This section will compare the performance of a range of passive adaptive policies.

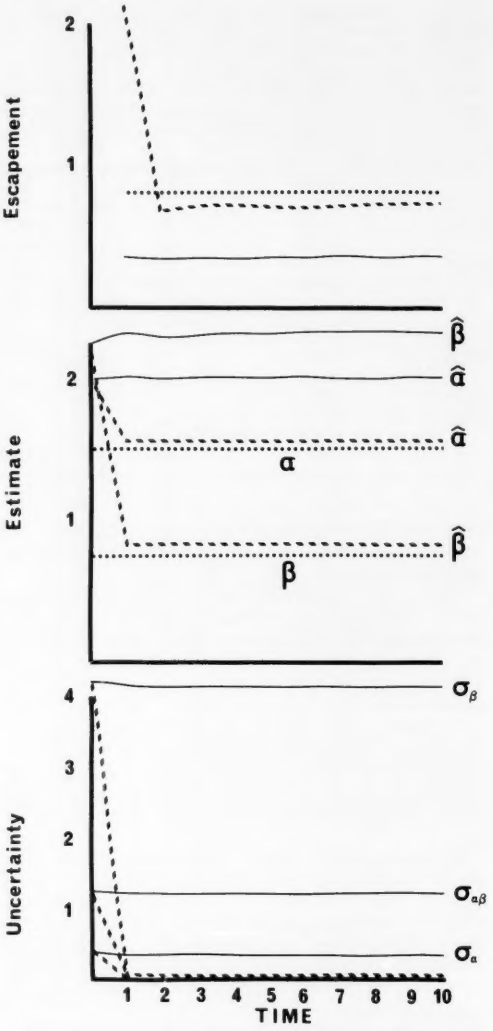

FIG. 9. Escapements chosen and resulting parameter estimates and uncertainties in a particular simulation for the case $\bar{S} = 0.3$, $S_s = 0.05$. Active adaptive policy (broken line), passive adaptive policy (solid line), optimal policy (dotted line): (a) escapements chosen; (b) parameter estimates; (c) uncertainty in parameter estimates.

The effect of infrequent updating of parameter estimates is shown in Table 3. The performance decreases as the frequency of parameter estimate updates is reduced, but the difference is not significant if the frequency is every eight generations or better. The effect on the estimation performance is inconsistent and is only clearly adverse in the case where there is only one parameter estimate update

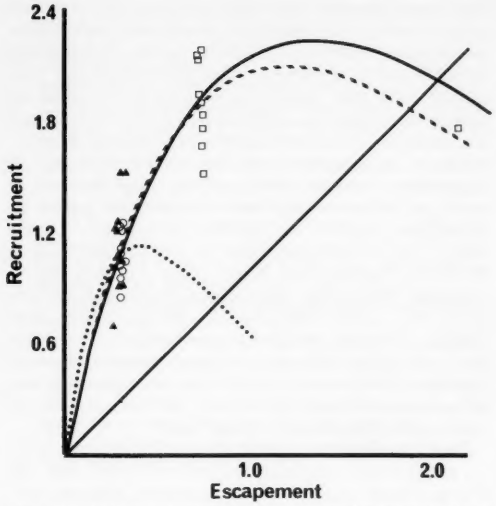

FIG. 10. Stock recruitment data in the same simulation as Fig. 9 generated by the active adaptive policy (open squares) and passive adaptive policy (open circles). The prior data are shown as solid triangles. The solid curve shows the true stock–recruitment relationship and the broken and dotted curves the estimated relationships after 10 yr for the active and passive adaptive policies, respectively.

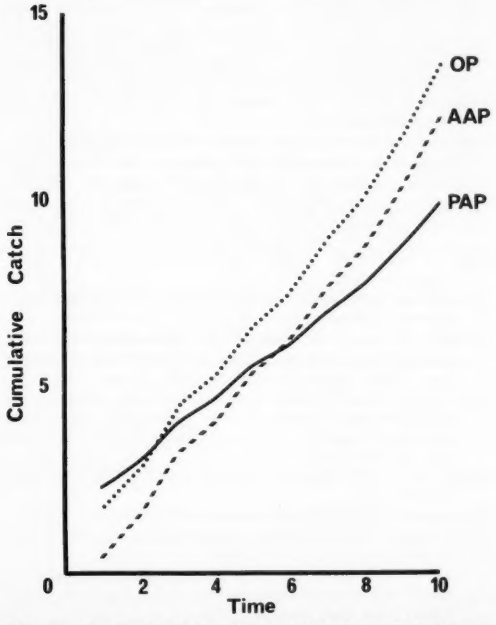

FIG. 11. Same simulation as Fig. 9 and 10. Comparison of cumulative catches for the optimal policy and the active and passive adaptive policies.

Table 3. Effect of infrequent update of parameter estimates. NYBU = number of years between parameter estimates updates; EO_L is the average performance relative to the optimal performance; α, β, and S^* are the mean errors in the estimates of the parameters and optimum escapement.

NYBU	EO_L	α	β	S^*
1	96.9	0.12	0.54	0.13
2	96.9	0.11	0.55	0.10
4	96.0	0.12	0.50	0.10
8	93.9	0.12	0.50	0.19
16	87.7	0.12	0.50	0.66
32	84.5	0.12	1.11	0.59

TABLE 4. Effect of reducing weight given to new data. GF = gain factor, the multiplicative factor on the prediction error gain in the regression; EO_L is the average performance relative to the optimal performance; α, β, and S^* are the mean errors in the estimates of the parameters and optimum escapement.

GF	EO_L	α	β	S^*
1	96.9	0.12	0.54	0.13
1/2	97.1	0.11	0.46	0.13
1/4	96.7	0.11	0.42	0.17
1/8	95.6	0.11	0.43	0.22
1/16	92.5	0.11	0.53	0.44
1/32	89.4	0.11	0.72	0.53
1/64	87.3	0.11	0.88	0.56
0	84.5	0.12	1.11	0.59

(NYBU = 16). This reflects the range of escapements over which observations will have been made.

The effect of weighting new data points on parameter estimates is shown in Table 4. The performance decreases as each point is given less and less weight. However, a significant difference in performance from the policy which gives full weight to the data is not obtained until the weight is reduced to $\frac{1}{16}$ the normal weight (GF = 0.0625). The performance in estimating the optimal escapement S^* corresponds closely with the average performance obtained.

The results of this section suggest that it is best to update parameter estimates as each new data point becomes available, giving full weight to the data in revising the estimates. The frequency of update and weight given to the data must be reduced substantially before a significant decrease in expected performance will occur. However, in individual cases the reduction in performance may be substantial.

Discussion

The main points to emerge from the comparison of performance by the range of adaptive policies are the following:

1) the average performance of the active adaptive policy is very high no matter what stock–recruitment data are initially available;

2) its performance in any particular case is also very good;

3) the improvement in performance of the active adaptive policy over the passive adaptive policy is occasionally dramatic;

4) the passive adaptive policy performs well except where the initial data are observed over a limited range of escape-

ments which spanned the apparently optimal escapement; and

5) the nonadaptive policy performs very well when the initial data include observations at high levels of escapement.

These results have several implications. The performance of the nonadaptive policy underlines a feature of adaptive control problems, that learning is only valuable to the extent that it increases overall performance. The very good performance of the nonadaptive policy, where escapements have been observed close to the unfished equilibrium level, suggests that probing by the active adaptive policy in such situations would not be worthwhile. However, the active adaptive control law shows that significant perturbations are still chosen (Fig. 1). Although the α and β estimates are greatly improved, the estimate of the optimal escapement S^* is not (Fig. 5), and there is no improvement in long-term catch to offset the loss in short-term yields. The active adaptive policy has not properly assessed the insensitivity of the optimal policy to uncertainty in the α parameter.

The passive adaptive policy performs well where the stock has apparently been consistently overexploited or underexploited. In either case, the escapement chosen by this policy is informative because it lies outside the range of escapements already observed and stands a good chance of identifying the correct parameter values. The active adaptive control law indicates that large perturbations, over and above those generated by the passive adaptive policy, should be chosen. Again, the value of these additional perturbations may be doubtful when weighed against the short-term loss in yield.

The conclusions which can be drawn on the basis of this study are limited to the extent that it is based on a highly simplified caricature of the problem of uncertainty in managing stock–recruitment systems. The issue of uncertainty about the functional form of the model used as a basis for management is not considered here nor are problems of changing parameters or errors in measuring escapement. A more realistic objective for management would include a penalty on high variability in catches. This would tend to generate more realistic active adaptive control laws, with strong deviations from the passive adaptive escapement only when this overlapped previous escapements.

The results presented are for one particular model, the Ricker model, and the question should be asked to what extent the value of active probing, to improve parameter estimates and long-term catch, is particular to that model. In this respect, the Ricker model is a useful first case, since it can be transformed so as to be linear in the parameters (eq. 3). This not only facilitates use of the active adaptive control algorithm (by simplifying the estimation problem) but also ensures that benefits of an active adaptive policy for more nonlinear models should be at least as great since it is known (Sorenson 1976) that there is no benefit to such a policy when the model is linear. (The Ricker model is linear with respect to the parameters, but not with respect to the state variable and parameters together.) The methodology can be applied in a similar fashion to the Schaefer model (Schaefer 1954, 1957) for situations where only catch and effort data are available. Extension to consideration of other, more highly nonlinear models is currently restricted by the ability to formulate suitable nonlinear estimation procedures.

Nevertheless, some important conclusions emerge from this study. Perhaps the most important is that passive adaptive policies can become locked into a situation where the same suboptimal escapement is chosen over and over again because it contains no information to show that it is, in fact, suboptimal. In the past, exploitation of many salmon stocks has been regulated more by economic factors than by biological considerations of the stocks themselves, resulting in observations of the response of the stock over a wide range of escapements. However, efforts at fixed escapement policies and better within season control systems have greatly decreased the variability in spawning stock levels in recent years. This is particularly true of key systems such as the Fraser, Skeena, and Rivers–Smiths Inlet in British Columbia. Washington State salmon escapements are now being very tightly controlled (S. Wright, Wash. Dep. Fisheries, Olympia, personal communication). This reduction in variability in recent years could become especially important if the parameters of the system are changing over time, because of changes in the biological characteristics of stocks and/or changes in the environment.

These considerations suggest that a deliberate active adaptive policy in managing stock–recruitment systems may well become crucial. This policy would involve deliberate perturbations away from constant escapement regimes, particularly towards higher escapements. Random variability, whether resulting from natural fluctuations and cycles in stock abundance, or from inability to control escapements or fishing effort, cannot be relied upon to provide the information to discriminate effectively between alternative hypotheses about stock dynamics.

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Appendix

Watt (1968) was among the first to point out that management of renewable resources could be regarded as a problem in optimization. Stochastic control theory provides techniques for the optimization of dynamic systems where controls are applied over a number of successive time periods. Such techniques might be usefully applied to the problem of managing a dynamic resource such as a fish stock.

To formulate a problem so that the techniques of stochastic control theory may be applied, four ingredients must be specified: a set of dynamic equations (a model of how the system changes over time); a set of measurement equations (how certain attributes of the system can be observed); a performance measure (defining the objectives of management); and a set of controls (the options for management). The stochastic control problem is to find the optimal sequence of control actions which minimizes (or maximizes) the performance measure subject to the dynamic constraints of the system.

The following four sections present the general formulation for each ingredient, followed by the specific formulation for the problem of managing a fish stock with uncertain Ricker stock–recruitment dynamics. The notation (k) denotes time or stage k in the ongoing management process up to stage N and symbols in bold print, e.g. $\mathbf{x}$, denote a vector, that is, $\mathbf{x}$ is the set of values $x_1, x_2, \ldots, x_n$.

THE DYNAMIC EQUATIONS

A system is considered whose state $\mathbf{x}$ changes over time according to the stochastic difference equation

$$\text{(A1)} \quad \mathbf{x}(k+1) = \mathbf{f}[\mathbf{x}(k), \mathbf{u}(k)] + \mathbf{v}(k) \qquad k = 0, 1, \ldots, N-1$$

where $\mathbf{u}(k)$ is the set of controls and $\mathbf{v}(k)$ is the system noise normally distributed with zero mean and covariance matrix $Q(k)$. The set of nonlinear functions $\mathbf{f}$ specifies how each element of $\mathbf{x}$ changes over time.

The Ricker model (eq. 1) can be cast in this form by expressing $S_t = R_t(1 - H_t)$, where H_t is a harvest rate, and taking natural logarithms:

$$\text{(A2)} \quad \ln R_{t+1} = \ln[R_t(1 - H_t)] + \alpha - \beta[R_t(1 - H_t)] + v_t.$$

If we define the elements of the state vector to be

$$x_1(k) = \ln R_t$$
$$x_2(k) = \alpha$$
$$x_3(k) = \beta$$

and the single element of the control vector $\mathbf{u}$ to be

$$u(k) = \ln(1 - H_t),$$

then the dynamic equations for the Ricker model can now be specified:

$$\text{(A3)} \quad \begin{aligned} x_1(k+1) &= x_1(k) + u(k) + x_2(k) \\ &\quad - x_3(k)\exp\{x_1(k) + u(k)\} + v(k) \\ x_2(k+1) &= x_2(k) \\ x_3(k+1) &= x_3(k). \end{aligned}$$

Notice that the uncertain parameters α and β have been included as state variables. Young (1974) has pointed out that the distinction between the states and parameters of dynamic systems is largely artificial. Parameters can be included as stationary or slowly varying state variables. In this case they are modeled as being stationary.

The set of equations (A3) is now of the same form as equation (A1), where the components of $\mathbf{f}$ are specified as

$$\begin{aligned} f_1[\mathbf{x}(k), \mathbf{u}(k)] &= x_1(k) + u(k) + x_2(k) \\ &\quad - x_3(k)\exp\{x_1(k) + u(k)\} \\ f_2[\mathbf{x}(k), \mathbf{u}(k)] &= x_2(k) \\ f_3[\mathbf{x}(k), \mathbf{u}(k)] &= x_3(k). \end{aligned}$$

The covariance matrix $Q(k)$ is given as

$$Q(k) = \begin{bmatrix} \sigma_v^2 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}$$

THE MEASUREMENT EQUATIONS

It is assumed that observations $\mathbf{y}(k)$ are available at each stage, and that the nonlinear measurement equation can be written in the form

$$\text{(A4)} \quad \mathbf{y}(k) = \mathbf{h}[\mathbf{x}(k)] + \mathbf{w}(k) \qquad k = 1, 2, \ldots, N$$

where $\mathbf{w}(k)$ is the measurement noise, normally distributed with zero mean and covariance $R(k)$. The set of nonlinear functions $\mathbf{h}$ specifies how each observation is related to the elements of the state vector $\mathbf{x}$.

For the problem considered in this paper, it is assumed that observations of the recruitment are available (eq. 2). Defining

the observation at each stage as

$$y(k) = \ell n R_t^{obs}$$

the measurement equation can be written as

(A5) $\quad y(k) = x_1(k) + w(k)$

where in this case the observation vector has a single element.

In the control theory formulation, it is assumed that the initial state $\mathbf{x}(0)$ is unknown, but an estimate $\hat{\mathbf{x}}(0)$ is available together with a measure of the uncertainty in this estimate, the error covariance matrix $P(0)$. The error covariance matrix is a generalization of the notion of variance about an estimate, for the case that the estimate is a vector quantity.

The Performance Measure

Optimal control theory considers a performance measure to be minimized of the form

$$\text{(A6)} \quad J = E\{L_N[\mathbf{x}(N)] + \sum_{k=0}^{N-1} L_k[\mathbf{x}(k), \mathbf{u}(k), k]\}$$

where $E\{\}$ denotes expectation over all the underlying random quantities. Thus the performance is a function L_N of the final state at the Nth stage, together with a function L_k of the series of states and controls over the preceeding time periods.

The objective considered in this paper is to maximize the sum of discounted catches over time. Noting that

$$C_t = R_t \cdot H_t = \exp\{x_1(k)\}\ [1 - \exp\{u(k)\}]$$

were C_t is the catch at time t, the functions L_N and L_k for the performance measure for this problem can be specified as

$$L_N[\mathbf{x}(N)] = \ell_1[x_1(N) - \ell_2]^2$$

$$\text{(A7)} \quad L_k[x(k), u(k), k] = -\exp\{x_1(k)\}\ [1 - \exp\{u(k)\}]\ [1/(1+d)]^k$$

where d is the discount rate per generation and ℓ_1 is a parameter that specifies the importance of being near a final value ℓ_2 at the end time N.

Admissable Controls

Control theory specifies that controls should be of the "feedback" type, i.e.

$$\text{(A8)} \quad \mathbf{u}(k) = u(k, Y^k, U^{k-1})$$

where $Y^k = \{\mathbf{y}(1), \ldots, \mathbf{y}(k)\}$ is the sequence of observations up to time k, and $U^{k-1} = \{u(0), \ldots, u(k-1)\}$ is the known sequence of past control actions. What this really means is that past information can be used to update state estimates at each stage before deciding on the control action to apply. For the problem considered here, this effectively means that controls (harvest rates) will be chosen based on past observations of recruitment and past escapements, that is, on the basis of the currently available information on the stock recruitment relationship. Having formulated the stochastic control problem, the task is to determine the sequence of controls $\{\mathbf{u}^*(k)\}$, $k = 0, 1, \ldots, N-1$ where each $\mathbf{u}^*(k)$ is of the form of equation (A8) such that the sequence minimizes the performance measure (A6) subject to the dynamic constraints (A1) and (A4).

The Dual Control Problem

The anticipation of future information by an active adaptive policy can be important because of the dual effect of applying a control to a system (Fel'dbaum 1960–61). On the other hand it may also affect future uncertainty about the state.

The potential effect of a control on uncertainty about a system is evident from examination of the problem considered in this paper. By controlling the harvest rate on a fish stock, management controls the escapement for that stock. However, it has already been shown that uncertainty about the parameters of the stock is determined to a large extent by the mean and variance of the escapements (eq. 4). Since the choice of escapement affects $\bar{S}$ and S_s^2, it can obviously affect the uncertainty about the stock–recruitment relationship.

Active adaptive policies have the feature of assessing the value of information by anticipating future feedback. Sorenson (1976) has shown that the optimal stochastic control policy should have this feature. The problem posed by the dual effect of control is that learning might conflict with the control purpose. For example, the most informative action might be to increase substantially the escapement, thereby reducing the catch and the short-term performance. The active adaptive policy must ensure that the learning is done only to the extent required by the overall performance.

Optimal Stochastic Control

The optimal control sequence $\mathbf{u}^*(k)$ for the problem formulated above can be obtained by applying Bellman's Principle of Optimality (Bellman 1961) in the information state. The information state is the set of observations Y^k and past control actions U^{k-1} up to the present time. For the Ricker model, this is the set of observed recruitments and known past escapements, that is, the available stock–recruitment data. The principle states that whatever the present information state and previous decisions are, the remaining decisions must constitute an optimal policy with regard to the present information state. Application of this principle generates a recursive system of equations which the optimal control must satisfy. The solution is obtained by considering the final stage problem and working backwards in time.

The information state can also be represented by the conditional probability distribution for the state, $P\{\mathbf{x}(k)/Y^k, U^{k-1}\}$. One example of such a probability distribution is the multivariate normal distribution. However, for nonlinear models the distribution is usually much more complex. If the information state is represented as a probability distribution, the solution of the optimal control problem will also require a set of recursive equations for updating this distribution. This is a nonlinear filtering problem and is solved, at least in theory, by applying Bayes' rule (Gelb 1974).

Wide-sense Adaptive Dual Control

Tse et al. (1973) point out three problems in trying to solve for the optimal control law. First, the information state may be of infinite dimension, in the case that the conditional probability distribution is used, or else is finite but grows with time, if the sequence (Y^k, U^{k-1}) is used. Second, the dynamic programming equations which result from application of the Principle of Optimality are not explicit functions and can only be solved numerically. Third, the determination of an optimal control law for any possible information state is limited by the "curse of dimensionality." Imagine having to calculate an optimal escapement for every single possible set of stock–recruitment data.

Using the same formulation outlined above, Tse et al. (1973) and Bar-Shalom and Tse (1976) developed an approximate solution to the optimal control problem which they called the wide-sense adaptive dual control algorithm. They propose that a reasonable suboptimal approach is to (1) approximate the information state by the mean $\hat{\mathbf{x}}(k)$ and covariance $P(k)$ of the state, thus reducing the dimensionality and keeping it constant over time; (2) approximate the dynamic programming equations, though their algorithm must still be solved numerically; and (3) calculate the optimal control "on-line," that is, only calculate control actions for information states which actually arise in the course of a particular problem. There need be no attempt to specify a control law for all possible information states.

In theory, this algorithm could be applied to any problem where the dynamic model can be formulated as a set of nonlinear stochastic difference equations of the form in equation (A1). In practice, the usefulness of this algorithm is limited by the ability to find a suitable nonlinear filter to update the estimates of the mean state $\mathbf{x}(k)$ and its associated error covariance matrix $P(k)$. Gelb (1974) discusses a number of such filters. In the case of the Ricker model, this problem was avoided because the parameter estimation problem can be linearized and the distribution of the state estimates can be obtained from the distribution of parameter estimates. This is also the case for the Schaefer model. For more nonlinear models, however, the estimation problem may well be limiting. This limitation applies not only to use of the wide-sense adaptive dual control algorithm, but also to the use of dynamic programming and other techniques which require a recursive method for updating probability distributions.

Effects of Measurement Errors on the Assessment of Stock–Recruitment Relationships

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Errors in measuring spawning stocks can have a profound effect on the appearance of stock–recruitment relationships. Large errors make recruitments appear to be independent of spawning stocks. This effect promotes overexploitation rather than simply making the relationship noisier and harder to measure. Efforts to explain variation in recruitment through factors other than spawning stock may be deceptive as well. Much fisheries theory and practice are based on the assumption that recruitment is largely independent of spawning stock; that assumption is not credible except in cases where spawning stocks are known to have been measured accurately.

Key words: stock, recruitment, statistics, overexploitation

WALTERS, C. J., AND D. LUDWIG. 1981. Effects of measurement errors on the assessment of stock–recruitment relationships. Can. J. Fish. Aquat. Sci. 38: 704–710.

Les relations stock–recrutement peuvent être profondément influencées par des erreurs de mesures des stocks reproducteurs. De grandes erreurs font que le recrutement semble être indépendant des stocks reproducteurs. Cet effet encourage la surexploitation plutôt que de simplement rendre la relation plus criante et plus difficile à mesurer. Il peut être tout aussi trompeur de faire appel à des facteurs autres que le stock reproducteur pour expliquer la variation du recrutement. La théorie et la pratique des pêches reposent surtout sur l'hypothèse que le recrutement est pour une bonne part indépendant du stock reproducteur; cette hypothèse manque de crédibilité, à moins qu'on ne soit certain que les stocks ont été mesurés avec précision.

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THE relationship between stock and recruitment is a central problem in fishery dynamics. Suggestions to deal with it range from pretending that it does not exist (assume recruits independent of spawners) to arcane "adaptive control" schemes for probing the underlying relationship through deliberate manipulation of harvest policies. Some workers (the artists among us) suggest drawing recruitment curves by eye, while others advocate objective statistical procedures for curve fitting. Still others observe all this with disgust and seek to explain recruitment variation as response to various environmental factors. Most of us have missed a very basic point that has been mentioned in the literature and which statisticians call the "errors in variables" or "structural relationship" (Kendall and Stewart 1973) problem: spawning stocks can rarely be measured or indexed without considerable sampling error, and observed values should therefore not be used as an independent variable in standard correlation and regression analyses. This paper will address some consequences of that statistical point.

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Recognizing Recruitment Overexploitation

Fisheries managers should be particularly concerned with the appearance of spawner recruitment data from stocks that are suffering "severe" recruitment overexploitation. By severe we shall mean any situation where, in the absence of sampling errors, each additional fish allowed to spawn will appear to contribute (on average) at least as many recruits as each spawner already being allowed. In the absence of depensatory mortality effects, this rather complicated definition translates into the simple recruitment relationship

$$(1) \quad \hat{r}_{t+1} = A\, s_t$$

where $\hat{r}_{t+1}$ is average total recruitment, s_t is the number of spawners one generation earlier, and A is recruitment per spawner. In the presence of depensatory effects, we expect to see the ratio $\hat{r}_t/s_{t-1}$ increasing (A not constant) with s_t.

A simple statistical test for severe overexploitation would be to regress linearly r on s for data collected during the suspect years. The intercept of this regression should be less than or equal to zero if severe overexploitation has occurred. If environmental effects are expected to be multiplicative

(more random variability at higher s), then a less-biased alternative would be to regress $\ln(r/s)$ on s. This regression should have a zero or positive slope if there has been severe overexploitation. The common objection to regressions of ratios, namely that a negative slope will be apparent even if r is completely independent of s, does not apply in this case; if r is independent of s, then recruitment overexploitation has not occurred, and we would actually want to see this reflected as a negative regression slope.

Most basic statistics texts warn that standard linear regressions are valid only if the independent variable (s in this case) is measured without error. Ricker (1973a, 1975; Appendix IV) and Peterman (1978) have recently carried the warning specifically to fisheries analysts. Much of what follows can be viewed as a demonstration of how important these warnings are to the fisheries manager.

Visual Appearance of Data from Overexploited Stocks

This section uses a simple simulation model to demonstrate the effect of spawning count errors on the appearance of stock recruitment data. The modeled population is always severely overexploited, as in equation (1), and is further subject to random environmental effects:

$$(2) \qquad r_{t+1} = s_t \, e^{\alpha + u_t}$$

where $s_t = r_t (1 - h_t)$, h_t is harvest rate, α is a productivity parameter, and u_t is a normally distributed random variable with mean 0.0 and variance σ_u^2 (representing effects of environmental variation). The assumption of normally distributed u is not critical to our argument, but can be justified theoretically on the grounds that survival from egg to recruitment is determined by a large number of nearby independent but variable risks. The harvest rate h_t is assumed to increase with r_t, so that population size is regulated by fishing, and the harvest rate exhibits some further variation unrelated to stock size. There are several ways to generate h_t with such properties; we simulate a collection of stocks each following equation (2) but having independent environmental effects, and h_t is then chosen so as to provide a fixed total escapement across the collection.

To generate "observed" data, we assume that spawning stocks are estimated with multiplicative errors:

$$(3) \qquad S_t = s_t \, e^{v_t}$$

where S_t is observed spawners, s_t is actual spawners, and v_t is a normally distributed random variable with mean 0.0 and variance σ_v^2. Observed recruitment is then estimated as $R_t = S_t + r_t h_t$, i.e. we assume that errors in estimating catch are insignificant. Various other assumptions about counting errors were also tested (i.e. $S_t = s_t (1 + w_t)$, w_t normally distributed or uniformly distributed); they produce essentially the same effect and will not be discussed further. The magnitude of counting errors implied by equation (3) can be most easily seen by example: for $\sigma_v^2 = 0.1$, 95% of S_t values will be between 0.54 s_t and 1.86 s_t; for $\sigma_v^2 = 0.5$, the 95% limits are 0.25 s_t and 3.97 s_t. Occasional errors of these magnitudes (i.e. off by a factor of 2 to 4) would not be considered unusual in most fisheries stock assessments, especially when the estimates are based on tagging studies.

Figure 1 shows "actual" and observed stock–recruit data for two simulation cases, both with $\sigma_u^2 = 0.1$ and $\sigma_v^2 = 0.25$. Because of counting errors, the observed spawning stocks appear to vary more widely than was actually the case. The visual effect on recruitment is dramatic: most observers would conclude in both cases that recruitment was independent of spawning stock. A more daring analyst might see a dome-shaped relationship in the first case, and would at least conclude that very high spawning stocks result in below-average recruitments.

We examined dozens of simulation cases, with σ_v^2 ranging from 0.01 to 0.5. It is hard to find objective criteria for visual distortion, but we noticed significant curvature in most "observed" relationships for which $\sigma_v^2 \geq 0.05$ (counting errors of roughly ±50%). For $\sigma_v^2 > 0.1$, we generally concluded that observed recruits were either independent of observed spawners or showed some dome-shaped relationship. In most cases where $\sigma_v^2 > 0.1$, the highest observed spawning stocks were associated with observed recruitments below average, and there was a tendency for the highest observed recruitments to occur at very low observed spawning stocks.

Patterns similar to the high variance cases are obtained when one plots successive pairs of "stock–recruit" points from a time series of completely independent observations (i.e. $R_t = \mu + w_t$ where μ is the population mean and $\text{cov}(w_t, w_{t+1}) = 0$). Eberhardt (1970) notes that such series will on average show an R_{t+1} vs. R_t correlation coefficient of −0.707. An intuitive explanation for Fig. 1 is that counting errors simply obliterate the stock–recruit relationship and replace it with a time series of nearly independent observations.

A common reaction by biologists faced with noisy stock–recruit data as in Fig. 1 has been to seek "environmental factors" that might explain variation in recruitment. Such efforts have not been particularly successful and could well be as deceptive as the stock–recruitment analyses that they seek to replace. Factors such as river flows (for Pacific salmon) and ocean temperatures may affect measurement processes as well as (or instead of) biological responses. As an obvious example, high river flows may cause difficulties in counting Pacific salmon spawners; underestimates of spawning would then lead to overestimates of recruits per spawner, and high river flows at spawning times would thus appear to have positive effects on spawning success.

Biases in Estimated Stock Recruitment Curves

One might argue that the deceptive patterns mentioned above are just visual illusions, and that objective statistical procedures should be used to detect the actual recruitment relationship. That is, one should assume some model for the relationship, then estimate the model's parameters from the data. If the model contains equation (1) as a special parameter case (i.e. $\beta = 0$ in Ricker model $r_t = s_{t-1} \, e^{\alpha - \beta s_{t-1}}$, or $\beta = 1$ in the power model $r_t = \alpha \, s_{t-1}^{\beta}$), then the parameter estimates should behave accordingly. That is, the null hypothesis of equation (1) should not be falsely rejected because of environmental fluctuations and observation errors.

It does appear possible to develop unbiased estimators for the parameters of simple stock–recruit models, given inde-

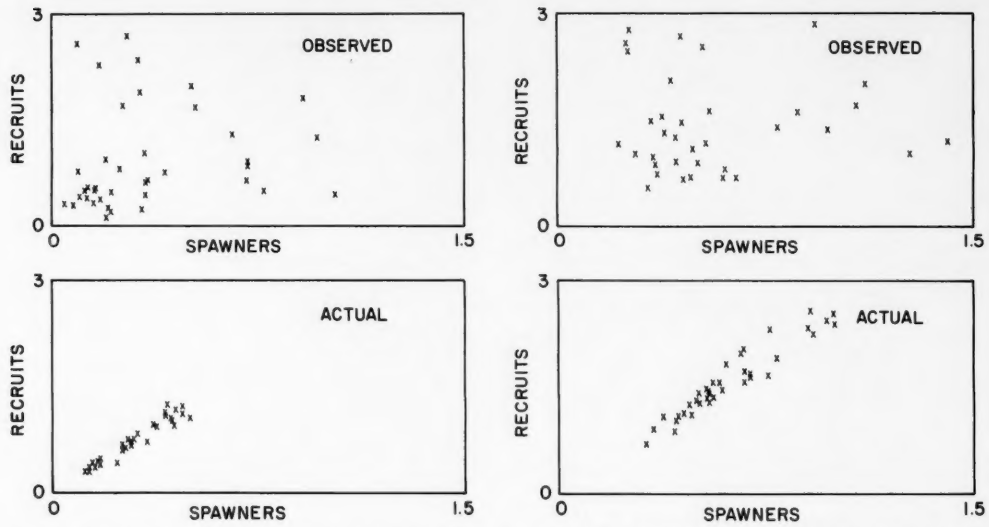

FIG. 1. "Actual" and observed stock–recruit relationships for two simulated populations that are severely overexploited. The actual data were generated with recruitment proportional to spawning stock; the observed data were generated by applying observation errors to the actual data.

pendent estimates of the observation error variance σ_v^2 (Ludwig and Walters 1981). However, standard least squares regression procedures, as advocated, for example, by Dahlberg (1973), Cushing and Harris (1973), and Walters and Hilborn (1976), are just as deceptive as visual examination of the data.

To illustrate what goes wrong with standard procedures, this section develops simple, consistent (asymptotically unbiased) estimators for two stock–recruitment models, and examines the bias in uncorrected estimators. The algebra will be somewhat involved, and general readers may skip the following without missing any basic arguments. The models to be examined are

$$r_j = s_{j-1}{}^{b}\, e^{a+u_j} \tag{4a}$$

$$r_j = s_{j-1}\, e^{a+bs_{j-1}+u_j} \tag{4b}$$

Here r_j denotes the number of recruits in generation j, and s_{j-1} denotes the number of spawners in the previous generation. The random survival of offspring is accounted for by u_j ($j=1,\ldots,n$), which are assumed to be independent, normally distributed random variables with mean 0 and variance σ_u^2. The parameters a and b which appear in (4) may be estimated by linear regression (Dahlberg 1973; Ricker 1975). Let

$$y_j = \ln r_j = a + b\, x_{j-1} + u_j, \tag{5a}$$

$$q_j = \ln (r_j/s_j) = a + bs_{j-1} + u_j, \tag{5b}$$

where

$$x_j = \ln s_j. \tag{6}$$

Then the method of least squares leads to equations for the power model:

$$\bar{y} = \hat{a} + \hat{b}\,\bar{x}, \tag{7a}$$

$$\hat{b} = \frac{C_{xy}}{C_{xx}}, \tag{8a}$$

and for the Ricker model:

$$\bar{q} = \hat{a} + \hat{b}\,\bar{s}, \tag{7b}$$

$$\hat{b} = \frac{C_{sq}}{C_{ss}}. \tag{8b}$$

Here the bar denotes the sample mean and C_{vv} denotes the sample covariance:

$$\bar{y} = \frac{1}{n}\sum_{j=1}^{n} y_j, \text{ etc.}, \tag{9}$$

$$C_{xy} = \frac{1}{n}\sum_{j=1}^{n} x_{j-1}\, y_j - \bar{x}\,\bar{y}, \text{ etc.} \tag{10}$$

The estimates $\hat{a}$ and $\hat{b}$ in (7) and (8) are consistent if r_j and s_j are uncontaminated by observation errors.

The Effect of Observation Errors

Now we assume as in the previous section that observations of r_j and s_j are subject to the same relative error (r estimated as catch plus escapement, no error in catch estimate). Let R_j and S_j denote the observed values. Then we write

$$R_j = r_j\, e^{v_j},\ S_j = s_j\, e^{v_j},\ Q_j = \ln (R_j/S_{j-1}), \tag{11}$$

$$X_j = \ln S_j,\ Y_j = \ln R_j,$$

where v_j are independent, normally distributed random variables, with mean 0 and variance σ_v^2.

We define the bias correction factor

(12) $B = \exp(\frac{1}{2}\sigma_v^2)$.

Then consistent estimates of a and b are given for the power model by

(13a) $\bar{Y} = a^* + b^* \bar{X}$,

where

(14a) $b^* = \dfrac{C_{XY}}{C_{XX} - \sigma_v^2}$

and for the Ricker model by

(13b) $\bar{Q} = a^* + b^* \bar{S}/B$, where

(14b) $b^* = \dfrac{[C_{SQ} + \bar{S}\,\sigma_v^2]\,B^3}{C_{SS} - \bar{S}^2\,(B^2 - 1)}$

Equations (13)–(14) are derived in the Appendix.

Equation (13a) has the same form as (7a); observation errors may be disregarded in that equation. However, the factor B in (13b) corrects a bias in $\bar{S}$, which is due to the nonlinear appearance of v_t in S_t. Similarly, the denominator in (14a) corrects C_{XX} by subtracting the variance of the observation error. Thus failure to correct for observation error affects the parameter estimates in two ways: it produces an overestimate of the information provided by the data. For the power model, both effects arise because, in expectation, the sample variance C_{XX} is biased by an amount σ_v^2. Also one usually has $C_{XY} > 0$, since density-independent recruitment corresponds to $b = 1$. Therefore, observation error generally leads to an underestimate of b^*, which in turn leads to an underestimate of the maximum sustainable yield (MSY) level of spawners. The observation errors encourage overexploitation, and they produce an illusion that this estimate is based upon more information than is actually present.

The interpretation of (14b) is more complicated. The denominator is analogous to the denominator of (14a). It is shown in the Appendix that

(15) $\lim_{n\to\infty} C_{ss} = \lim_{n\to\infty} [C_{SS} - \bar{S}^2\,(B^2 - 1)]/B^4$.

That is, (15) provides a consistent estimate of the denominator of (8b). The term $\bar{S}\sigma_v^2$ in the numerator of (14b) corrects the effect of correlation between errors in Q and in S; the additional factor B corrects the bias in $\bar{S}$, as in (13b).

The direction of bias in the uncorrected estimate of b is not clear from (14b). This uncorrected estimate $\hat{b}$ is given in analogy with (8b):

(16) $\hat{b} = \dfrac{C_{QS}}{C_{SS}}$.

It is shown in the Appendix that

(17) $\lim_{n\to\infty} (\hat{b} - b) = \lim_{n\to\infty} -b[(1 - B^{-2}) + \dfrac{1-B^{-2}}{B}\dfrac{\bar{S}^2}{C_{SS}}] - \sigma_v^2 \dfrac{\bar{S}}{C_{SS}}$.

Since $B > 1$, the coefficient of b on the right-hand side of (17) is positive. Thus if $b < 0$ (as would usually be the case), then the two terms on the right-hand side of (17) will have different signs. However, if b is small (if there is weak density dependence), then the right-hand side of (17) is negative. Therefore, if density dependence is weak, the effect of observation errors is to overestimate the amount of density dependence. This leads to overexploitation, as was the case for the power model. On the other hand, if density dependence is strong ($-b$ is large), then observation errors lead to underexploitation.

Effects on Adaptive Performance

Biases in stock/recruit parameter estimates do not automatically imply poor management of harvests. The biases might cancel one another in assessments of optimum escapements, or the optimum might be relatively insensitive to the parameter estimates. For example, optimum escapements estimated by the Ricker model are relatively insensitive to the α parameter. Further, the observed exploitation history can have a profound effect on performance of any statistical procedure. If data are available only since the stock has become heavily exploited (i.e. all observed spawning stocks relatively low), estimation performance would be generally much poorer than for cases where data are also available from the early development of the fishery (Hilborn 1979).

To see more clearly the management effects of biases, we elected to simulate the performance of a "naive adaptive manager." The manager is faced with a population that behaves according to the Ricker stock–recruitment model (eq. 4b), with "actual" parameters $a = 1$, $b = 1$, and $\sigma_u^2 = 0.25$ (random environmental effects are quite large). He is given an initial exploitation history of five stock/recruit data points. Two cases are considered: in the first, his historical data represent only a period of high exploitation, where the initial recruitment $R_0 = 0.1$ and the historical exploitation rate has been 0.8 on each of the five cycles. In the second, his record involves a development history where $R_0 = 1.0$, and the sequence of past exploitation rates has been 0.1, 0.2, 0.3, 0.4, and 0.5.

After each cycle, the naive manager is assumed to know the catch exactly, and to estimate the spawning stock with a multiplicative error as in equation (3). He then has one more stock/recruit data point and proceeds to update his estimates of the Ricker model parameters by applying the usual linear regression equations (eq. 7–8) uncorrected for the spawning count errors.

He then uses the updated parameter estimates and the last spawning stock observation to "forecast" the next recruitment, and estimates the best spawning stock to allow. Here he operates as a passive adaptive manager (Walters and Hilborn 1978); he assesses the best spawning stock according to the equations in Ricker (1975), which do not account for uncertainties. He then estimates an exploitation rate $h_t = (\hat{R}_t - \hat{S}_t^*)/\hat{R}_t$, where R_t is his forecast recruitment and S_t^* is his estimated optimum spawners. It is assumed that he can achieve this rate exactly; his catch is then $h_t R_t$ (rather than $\hat{R}_t - \hat{S}_t^*$).

In Table 1 results from Monte Carlo simulations for the two-population history cases and for three levels of counting

TABLE 1. Performance measures for a naive adaptive manager who does not account for errors in spawning stock estimates.

Average estimates from 10 simulations over 20 generations each (ranges in parentheses)	Population initially overexploited counting error variance			Population initially unharvested counting error variance		
	0.0	0.0625	0.25	0.0	0.0625	0.25
20-yr catch	4.00 (2.14–6.65)	3.33 (1.57–5.32)	2.62 (1.21–5.02)	6.69 (4.75–8.41)	6.56 (4.61–8.58)	5.90 (3.88–8.09)
Ricker α parameter (at generation 20)	1.04 (0.90–1.13)	1.12 (0.93–1.39)	1.24 (1.02–1.53)	1.03 (0.85–1.38)	1.12 (0.98–1.46)	1.25 (1.04–1.58)
Ricker β parameter (at generation 20)	1.12 (0.62–1.86)	2.79 (0.70–9.07)	4.57 (0.61–13.4)	1.03 (0.59–1.66)	1.15 (0.77–1.77)	1.32 (0.92–1.83)
"Optimum" escapement (at generation 20)	0.44 (0.71–0.66)	0.34 (0.11–0.66)	0.25 (0.05–0.71)	0.45 (0.34–0.65)	0.42 (0.31–0.55)	0.40 (0.27–0.57)

error are summarized. To simplify comparisons, the same sequences of random numbers were used to generate environmental effects and counting errors for each combination of population history and counting error variance (the random sequence was different from simulation trial to trial for each combination).

Table 1 indicates that the initial data history is a more important determinant of management performance than are biases associated with counting errors. If the historical data have all been collected at low stock sizes, the passive adaptive manager has trouble initially in estimating the equilibrium stock size (though he usually achieves a good estimate by generation 20 in the absence of counting errors) and must give up catches during the recovery period as well. Counting errors have a devastating effect on his ability to "see" that the stock has been overexploited in the first place, and on average he is still using a spawning stock that is almost 50% too low after 20 cycles.

The naive manager generally fares much better when he faces a data history of developing exploitation. The biases in his parameter estimates are not severe even when counting errors are large, and his estimate of the optimum spawning stock is usually quite good after 20 cycles. However, these results should be viewed with caution. In practice, the early development history of a fishery is likely to involve considerable changes in counting methods (and thus σ_v^2) and the actual stock parameters are likely to change as unproductive substocks are reduced (Ricker 1973b).

Discussion

Since a severely overexploited stock can appear to behave like the examples in Fig. 1, it is obvious that the fishery manager should not trust models based on the assumption that recruitment is independent of spawning stocks, at least until he can clearly demonstrate that spawning stocks have been measured "accurately" (i.e. errors less than ±30% or so). Such demonstrations are rare in the fishery literature. For most salmon stocks in British Columbia, the data recording system alone generates unacceptably large errors; counts are recorded only by abundance classes, and the midpoint of the class is taken to be the best estimate. With a bit of digging, we could probably demonstrate comparable errors for other fishery data sets. A basic point is that stock and recruitment data sets should not be published or used unless they are accompanied by estimates of measurement error variance; otherwise they are meaningless and misleading.

Many researchers have taken for granted that recruitment is largely independent of spawning stock, and have gone on to seek other mechanisms to explain apparent variation. It is frightening to realize that much of this work may be directed to explaining patterns that do not exist in the first place.

We do not mean to imply that recruitment is often strongly dependent on spawning stock, just because evidence to the contrary can be misleading. In fact, the analysis leading to Fig. 1 suggests an interesting model for how recruitment can actually be independent of total spawning stock over a wide range of stock sizes. Suppose total spawners are measured very accurately, but that only a randomly variable and unobserved proportion of these spawners are actually successful. Suppose that each successful fish produces (on average) the same number of recruits, and that there is no effect of density on survival to recruitment. (Such a population would have to be regulated either by fishing or by some compensatory mechanism that is not exhibited over the range of observed stock sizes.) Then data like Fig. 1 will result where recruits are plotted against total spawners; in effect total spawners give a poor estimate of the actual number of spawners participating in the density-independent recruitment process. Suppose further that the successful spawners in any year represent particular genotypes whose eggs and fry carry the right mix of temperature-sensitive enzyme alleles to develop successfully in the temperature regime prevalent that year. Then from year to year, temperature will appear to have some effect on recruitment, but the response will be inconsistent because of changes in gene frequencies in the total spawning population. In this system, the scientist who seeks environmental correlates of recruitment (as a prelude to pursuing more detailed research) may fail to recognize either spawners or temperature as key factors.

It is time for a thorough reexamination of the evidence regarding stock and recruitment in fisheries. We can suggest procedures to help correct for measurement errors (Ludwig and Walters 1981), to make some historical data sets more usable for management. But the real need is for functional rather than correlative studies on factors affecting the re-

cruitment process, and for careful analyses of measurement errors and means to reduce them.

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Appendix

Derivation of Consistent Parameter Estimates

1. Power Model

The basic regression equation is (5a), but the observed quantities are given by (11). These equations imply that

$$(18)\quad Y_j = a + b X_j + u_j + v_j - bv_{j-1}, \qquad j = 1,\ldots,n.$$

If Y_j is averaged over the observations, the result is

$$(19)\quad \bar{Y} = a + b\bar{X} + \bar{u} + \bar{v} - b\bar{v}_-,$$

where

$$(20)\quad v_- = \frac{1}{n}\sum_{j=1}^{n} v_{j-1}.$$

Each of the random variables $\bar{u}$, $\bar{v}$, and $\bar{v}_-$ has mean zero and variance proportional to $\frac{1}{n}$, by our assumptions. Therefore

$$(21)\quad \lim_{n\to\infty} \bar{Y} = a + b \lim_{n\to\infty} \bar{X}.$$

If Y_j is multiplied by x_j before averaging, the result is

$$(22)\quad \overline{XY} = a\bar{X} + b\,\overline{XX} + \overline{uX} + \overline{vX} - b\,\overline{v_-X}.$$

If (19) is multiplied by $\bar{X}$ and subtracted from (22), we obtain

$$(23)\quad C_{XY} = b\,C_{XX} + C_{uX} + C_{vX} - b\,C_{v_-X}.$$

where the sample correlation coefficients are defined by (10). By our assumption, u and x are uncorrelated, and v and x are uncorrelated. However,

$$(24)\quad \lim_{n\to\infty} C_{v_-x} = \sigma_v^2.$$

Therefore

$$(25)\quad \lim_{n\to\infty} C_{XY} = b \lim_{n\to\infty} (C_{XX} - \sigma_v^2).$$

Equations (21) and (25) imply that (13a) and (14a) provide consistent estimates.

2. Ricker Model

Equations (5b) and (11) imply that

$$(26)\quad Q_j = a + b\,s_{j-1} + w_j - v_{j-1}, \qquad j=1,\ldots,n,$$

where

$$w_j = u_j + v_j.$$

If Q_j is averaged over the observations, the result is

$$(28)\quad \bar{Q} = a + b\bar{s} + \bar{w} - \bar{v}.$$

As in the previous case,

$$(29)\quad \lim_{n\to\infty} \bar{Q} = a + b \lim_{n\to\infty} \bar{s}.$$

In view of (11) and (12),

$$(30)\quad \lim_{n\to\infty} \bar{S} = B \lim_{n\to\infty} \bar{s}.$$

Therefore

$$(31)\quad \lim_{n\to\infty} \bar{Q} = a + b \lim_{n\to\infty} \bar{S}/B.$$

If (27) is multiplied by S_{j-1} before averaging, the result is

$$(32)\quad \overline{QS} = a\bar{S} + b\,\overline{sS} + \overline{wS} - \bar{v}_-\bar{S}.$$

If (28) is multiplied by S and subtracted from (32), we obtain

$$(33)\quad C_{QS} = b\,C_{sS} + C_{wS} - C_{v_-S}$$

By our assumptions,

$$(34)\quad \lim_{n\to\infty} C_{wS} = 0,$$

$$(35)\quad \lim_{n\to\infty} C_{v_-S} = \lim_{n\to\infty} \bar{s}\,E(v\,e^v) = \lim_{n\to\infty} \bar{s}\,B\,\sigma_v^2$$
$$= \sigma_v^2 \lim_{n\to\infty} \bar{S},$$

$$(36)\quad \lim_{n\to\infty} C_{sS} = B \lim_{n\to\infty} C_{ss},$$

$$(37)\quad \lim_{n\to\infty} C_{SS} = \lim_{n\to\infty} [B^4 (C_{ss} + \bar{s})^2 - B^2\,\bar{s}^2],$$

equation (37) implies (15). When (34)–(37) are substituted into (33), the resulting equation implies (14b).

To derive (17), we substitute (16) into (14b). Thus

$$(38)\quad \lim_{n\to\infty} [C_{SS} - \bar{S}^2 (B^2 - 1)]\,\frac{b}{B^3} = \lim_{n\to\infty} [\hat{b}\,C_{SS} + \bar{S}\,\sigma_v^2].$$

After rearrangement, (38) implies

$$\lim_{n\to\infty}[(\hat{b}-b)\,C_{ss}] = \lim_{n\to\infty}\{-b\,[\bar{S}^2\,\frac{B^2-1}{B^3} + C_{ss}\,(1-\frac{1}{B^3})\} - \bar{S}\,\sigma_v^2\}. \tag{39}$$

Then (39) implies (17). There must be an easier way to make a living.

Measurement Errors and Uncertainty in Parameter Estimates for Stock and Recruitment

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A procedure is developed for estimating stock and recruitment parameters in the presence of measurement errors. It requires an independent assessment of the ratio of environmental and measurement error variances, and provides maximum likelihood estimates of the time series of errors as well as the average stock–recruit parameters. Measures of parameter uncertainty are also provided and are incorporated into an analysis of optimum spawning stocks. This analysis indicates that much higher, or at least more variable, spawning runs should be allowed in many Pacific salmon stocks. An immediate need in salmon management is to obtain estimates of the measurement error variance, so that recent historical data can be made more useful.

Key words: statistics, stock recruitment, optimum spawning, uncertainty

LUDWIG, D., AND C. J. WALTERS. 1981. Measurement errors and uncertainty in parameter estimates for stock and recruitment. Can. J. Fish. Aquat. Sci. 38: 711–720.

Nous avons mis au point un méthode d'estimation des paramètres de stock et de recrutement quand les mensurations comportent des erreurs. La méthode est fondée sur une évaluation indépendante du rapport entre les variances de l'environnement et celles des mensurations, et donne des estimations de probabilité maximale de la série temporelle d'erreurs, de même que les paramètres moyens de stock et de recrues. Nous fournissons également des mesures de l'incertitude des paramètres, mesures incorpores dans une analyse de stocks reproducteurs optima. A la suite de cette analyse, on constate que, dans plusieurs stocks de saumons du Pacifique, il faudrait prévoir des remontées reproductrices beaucoup plus fortes, ou du moins plus variables. Dans la gestion du saumon, il faudrait tout d'abord estimer la variance des erreurs de mensurations, de façon à tirer meilleur profit des données historiques récentes.

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MEASUREMENT errors may have two effects upon the assessment of stock and recruitment: (1) the parameter estimates may be inconsistent, as a result of hidden correlations in the regression equations, and (2) the amount of information available may be overestimated. These effects are pointed out by Walters and Ludwig (1981). Here we extend that analysis to take account of the limited number of observations which are usually available. We develop a more elaborate estimation procedure and further explore the policy consequences of measurement errors.

A major conclusion of Walters and Ludwig is that estimates of numbers of spawners and recruits are of little value unless the accuracy of the estimates is also assessed. There is a parallel principle in the statistical estimation of model parameters: the statistical estimates are of little value unless they are accompanied by estimates of their accuracy. A similar principle applies to management decisions which are based (in part) upon parameter estimates: uncertainty about parameter values cannot be ignored in formulating management policy. These principles are valid even if observations are made with perfect accuracy. However, large observation errors (which are present in most fisheries data) result in substantial uncertainty in parameter estimates. The parameter uncertainty frequently overwhelms effects of density dependence in the stock–recruitment relationship. In such situations, more information is required before a rational strategy can be determined. Then the first task of the manager is to obtain such information. This will usually require purposeful manipulation of the number of spawners.

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Estimation of Observation Errors

We shall illustrate our procedure with the Ricker model. Other models are treated in the Appendix. If r_j and s_j denote

the actual number of recruits and spawners in generation j, we assume that

$$(1) \quad r_j = s_{j-1}\, e^{a+b\, s_{j-1} + u_j},$$

where u_j are independent, normally distributed random variables, with mean 0 and variance σ_u^2. The observed numbers of recruits and spawners are given by R_j and S_j, respectively, where

$$(2) \quad R_j = r_j e^{v_j},\ S_j = s_j e^{v_j}.$$

Here v_j are independent, normally distributed, random variables with mean 0 and variance σ_v^2. Notice that the same relative error appears in numbers of recruits and spawners of a given generation. (Recruits are usually estimated as catch plus spawners, and we assume catch is measured with small error.) Our method can also be applied if the relative errors are different, but details will not be given here.

Given observations (R_j, S_j) for generations $j = 0, 1, 2, \ldots, n$, we seek to estimate the parameters a, b, σ_u^2, and σ_v^2 from these observations. It is shown in Kendall and Stewart (1973) that this problem is insoluble unless additional information about the errors is provided. We have chosen to prescribe the ratio

$$(3) \quad \lambda = \frac{\sigma_v^2}{\sigma_u^2}.$$

That is, all of our calculations depend upon the value of λ, which must be chosen beforehand. Other assumptions might be made, but this one leads to a relatively straightforward estimation procedure.

Once λ is prescribed, the parameters a, b, σ_u^2, and $v_0, v_1, \ldots, v_n$ may all be estimated by the method of maximum likelihood. Details are given in the Appendix. The logarithm of the likelihood of the observations is given by

$$(4) \quad L(a, b, \sigma_u^2, v_0, \ldots, v_n) =$$

$$-\frac{1}{2\sigma_u^2}\left[\sum_{i=1}^{n} u_i^2 + \frac{1}{\lambda} v_i^2\right] - n \ln \sigma_u - (n+1)\ln(\lambda\sigma_u),$$

where $u_1, \ldots, u_n$ are determined from (1) and (2). All of the parameters except for σ_u^2 are determined by maximizing L. If σ_u^2 were determined in the same way, the estimate would be biased; σ_u^2 can be estimated from the residual sum of squares:

$$(5) \quad \hat{\sigma}_u^2 = \frac{1}{2n + 1 - (n+3)}\left[\sum_{i=1}^{n} \hat{u}_i^2 + \frac{1}{\lambda}\sum_{i=0}^{n} \hat{v}_i^2\right],$$

where $\hat{u}_i$ and $\hat{v}_i$ are the estimated values which maximize L.

The results of this procedure are illustrated in Fig. 1. The original data points are displayed, together with the best least squares fit with the Ricker model. The corrected data points are obtained from (2), where v_j are estimated by the maximum likelihood procedure with $\lambda = 1$. In Fig. 1, the original points are shown as numbers representing spawning years. They are joined to stars representing corrected points. Best fits to original and corrected data are shown for the Ricker model.

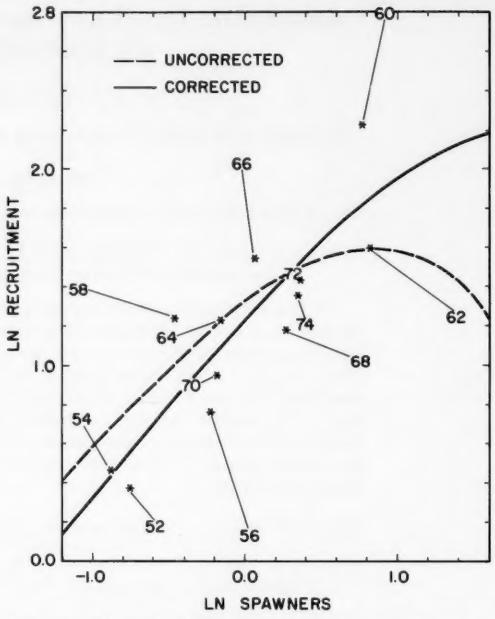

FIG. 1. The logarithm of the number of recruits in generation n is plotted against the number of spawners in generation $n-1$, for pink salmon in British Columbia statistical area 8. The original data points are plotted as numbers, which represent spawning years. The broken line curve is the best fit to the data, using the Ricker model. If observation errors are considered, whose variance is equal to the variance of the annual fluctuations in recruitment, then the original data points are corrected to the values shown with stars. The solid curve is the best fit to the corrected data, using the Ricker curve. The corrected slope is generally higher than the uncorrected slope, because of hidden correlation in the original data.

To assess the validity of the procedure, we have applied it to artificial data, starting with parameters $\hat{a}$, $\hat{b}$, and $\hat{\sigma}_u^2$ as estimated in Fig. 1. For the artificial data, s_i, $i = 0, \ldots, n-1$ were chosen such that $\ln s_i$ were uniformly distributed on an interval of width w, with the same center as for the original data. An important parameter is w, since it measures the amount of information provided about variation of the number of recruits with the number of spawners. Then sequences $\{u_i\}$ and $\{v_i\}$ were generated to be normally distributed with mean 0 and variance σ_u^2 and σ_v^2, respectively. The values of σ_u^2, σ_v^2, a, and b were those determined as in Fig. 1. Then (1) and (2) were used to generate the artificial data, subject to the constraint that $s_i \le r_i$. The result of all this is a set of artificial data which resembles the original data, but for which the parameters are known. The amount of information in the artificial data is controlled by the number of points n, and the width w.

Figures 2 and 3 illustrate the results when the estimation procedure was applied to such artificial data sets, while assuming the correct value of $\lambda = 1$. In some cases, as in Fig. 2, the error corrections led to very accurate estimates. Fre-

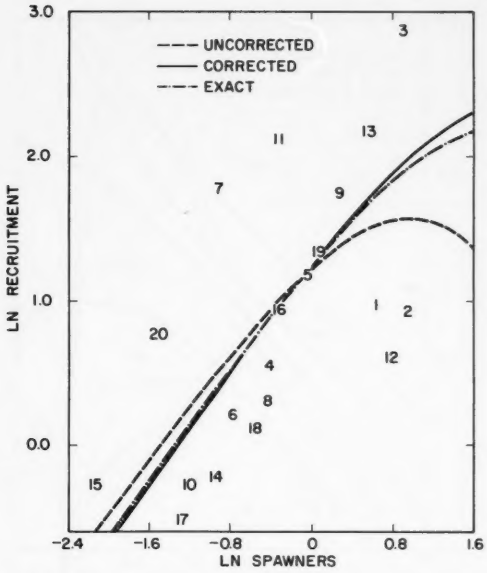

FIG. 2. Simulated stock and recruitment data, for the parameters estimated in Fig. 1. The curve labeled "exact" is the corrected fit from Fig. 1. The curve labeled "uncorrected" was the best fitting Ricker curve to the simulated data. The curve labeled "corrected" was obtained by assuming the observation errors had the same variance as the variance of annual fluctuations in recruitment.

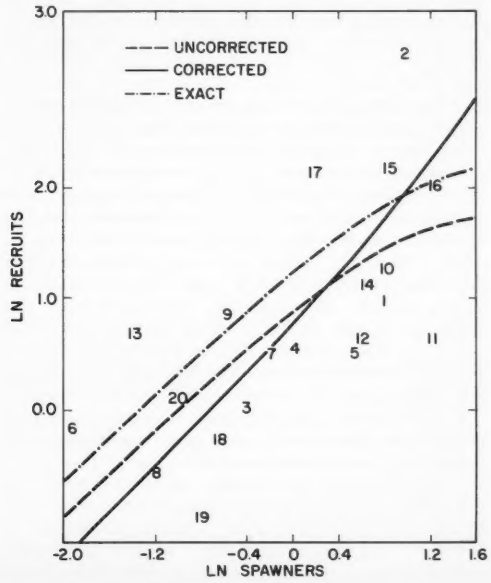

FIG. 3. A second set of simulated data, obtained under the same conditions as in Fig. 2.

quently, as in Fig. 3, the results were far from accurate, and the error correction did not improve the accuracy. For very large data sets ($50 \leq n \leq 100$) the error correction was more accurate and reliable. Although such an outcome is reassuring, it is irrelevant to most management problems, since such large sets are not yet available (and would be unreliable anyway, because of changes in stock parameters).

It is more important to assess the validity of the procedure if $10 \leq n \leq 20$. In this range, the width w has a decisive impact upon the estimates. Accuracy and reliability were both poor for widths w comparable to those available for historical British Columbian salmon data. Accuracy increased sharply if the width w was increased by a factor of 2 to 4, even if no observation error correction was used. This result emphasizes the need for management strategies which produce larger variations in the actual number of spawners.

Uncertainty in Parameter Estimates

The unreliability of the estimation procedure when applied to artificial data shows the need for estimates of parameter uncertainty. One approach would be to describe the distribution of the least squares estimates for large samples. However, fisheries managers are not confronted with many independent sets of data drawn from the same population, so the basic assumptions which underlie the conventional approach to estimation are not satisfied. On the contrary, the manager usually has one set of observations for each stock, and data from differing stocks will seldom have the same statistical properties.

A more appropriate procedure is to base all statistical inference upon the likelihood of the given observations, as a function of the parameters to be estimated. Such an approach has been adopted implicitly in equation (4), where the logarithm of the likelihood of the observations is displayed as a function of these parameters. The actual likelihood function will be extremely complicated. However, we may approximate it by a quadratic function, in the vicinity of the maximum likelihood estimates. As shown in the Appendix, the result is an approximation

$$(6) \quad L(a,b) \sim L(\hat{a}, \hat{b}, \hat{\sigma}_u^2, \hat{v}_0, \ldots, \hat{v}_n) - \frac{1}{2\sigma_u^2}[M'_{aa}(a-\hat{a})^2 + 2M'_{ab}(a-\hat{a})(b-\hat{b}) + M'_{bb}(b-\hat{b})^2].$$

The coefficients $(M'_{aa}, M'_{ab}, M'_{bb})$ are derived from a reduced information matrix, which takes account of variation of the estimated errors $v_0, \ldots, v_n$ with the parameters $\hat{a}$ and $\hat{b}$.

Up to this point, the calculations are hardly different from a conventional large-sample approach. The same information matrix appears in describing the distribution of the maximum likelihood estimates. However, we believe that it is more appropriate to regard (6) as the probability density function of the parameter values, based upon the information provided by the data. That is, the likelihood function describes the state of our knowledge of the parameter values, as determined by the observations. A difficulty with this Bayesian approach is that other information about the parameter values should be incorporated into a "prior distribution," which would multiply the likelihood. Such a prior distribution in essence incorporates

additional (less-accurate) observations which are assigned lesser weight than the others. This possibility is considered in the Appendix. If equal weights are assigned to all observations and the likelihood function is used to describe the parameter distribution, this is equivalent to adopting a uniform, uninformative, prior parameter distribution.

Now the stock–recruitment relation (1) must be re-examined. If a and b are random variables distributed as in (6), then (1) takes the form

$$\hat{r} = s\, e^{\hat{a} + \hat{b}s + u + z}, \tag{7}$$

where z is a random variable which accounts for the possible deviation of (a, b) from $(\hat{a}, \hat{b})$. If the approximation (6) is used, then $a + bs$ is a normally distributed random variable with mean $\hat{a} + \hat{b}s$, and with variance

$$\sigma_z^2(s) = C_{aa} + 2s\, C_{ab} + s^2 C_{bb}. \tag{8}$$

The parameter covariance matrix C is obtained from the inverse of the information matrix:

$$\begin{bmatrix} C_{aa} & C_{ab} \\ C_{ab} & C_{bb} \end{bmatrix} = \sigma_u^2 \begin{bmatrix} M'_{aa} & M'_{ab} \\ M'_{ab} & M'_{bb} \end{bmatrix}^{-1} \tag{9}$$

Uncertainty about the stock–recruitment relationship may be visualized by drawing two confidence intervals for $\ln \hat{r}$. In the first of these, we ignore year-to-year fluctuations in recruitment, which are expressed by u. Then an approximately 50% confidence interval will have width $\sigma_z(s)$ around the maximum likelihood estimate $\hat{r}$:

$$\hat{r} = s\, e^{\hat{a} + \hat{b}s} \tag{10}$$

The second interval takes the year-to-year fluctuations into account, and has width $\sqrt{\sigma_u^2 + \sigma_z^2(s)}$. These intervals are shown in Fig. 4, for the data of Fig. 1. Uncertainty is least in locating the "center of mass" of the data points. However, the slope of the fitted curve is much less certain. The same, or similar intervals would be drawn, even if a Bayesian approach were not adopted.

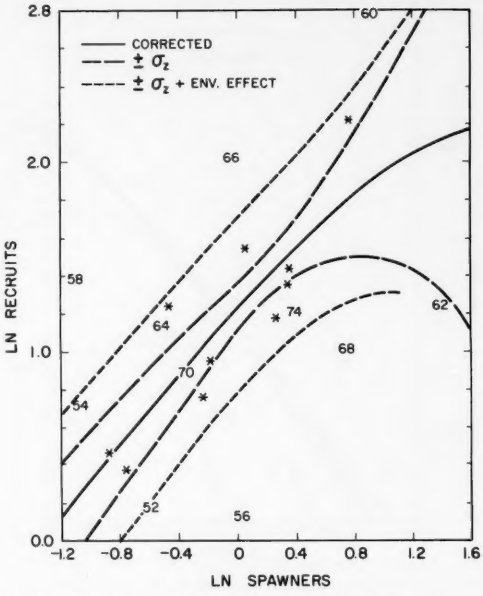

FIG. 4. Confidence intervals for the stock–recruitment relation, as fitted from the data of Fig. 1. The original data, the corrected data, and the solid curve are as shown in Fig. 1. The inner pair of broken line curves are separated by one standard deviation $\sigma_z(s)$, as defined in eq. (8). Thus the probability is ~50% that the correct (averaged) stock–recruitment relation will be between these curves, above any given point on the $\ln s$ axis. The outer pair of broken line curves show one standard deviation if the effects of year-to-year fluctuation are included.

Management in the Presence of Uncertainty

It is clear from Fig. 4 that the effect of parameter uncertainty increases sharply at the ends of the spawner range where data are available. In most cases that we have examined, the effect is most pronounced at the upper end of that interval. Thus extrapolation of the stock–recruitment relation to such higher values is not warranted: on the basis of the data, we usually cannot predict the effect of a substantial increase in the number of spawners. Therefore, some unlikely possibilities may have large positive or negative effects on the expected performance of a given management strategy.

To focus the discussion, we shall consider policies which set escapement targets: if q is the target escapement, then $r - q$ of the recruits are harvested if $r > q$, and no harvesting is done if $r < q$. Such a policy cannot usually be achieved in practice, nor would it necessarily be most desirable. However, such policies have been shown to produce maximum expected yields (Mendelssohn 1979; Reed 1974; Walters 1981). They are useful as a standard of comparison with other policies, and only one parameter (q) specifies the policy.

How should q be determined? A simple approach is to compare the expected yield at equilibrium for each value of q. If parameter uncertainty is ignored, then we have

$$\hat{H}(q) = \underset{u}{E}\left[q\, e^{\hat{a} + \hat{b}q + u}\right] - q = q\, e^{\hat{a} + \hat{b}q + \frac{1}{2}\sigma_u^2} - q. \tag{11}$$

Then we determine $\hat{q}$ in such a way that $\hat{H}(q)$ has a maximum at $q = \hat{q}$.

If we account for current parameter uncertainty but not the effect of q on future uncertainty, then the expectation in (11) is taken over the distribution of z as well as u. Thus

$$\bar{H}(q) = \underset{u,z}{E}\left[q\, e^{\hat{a} + \hat{b}q + u + z}\right] - q = q\, e^{\hat{a} + \hat{b}q + \frac{1}{2}\sigma_u^2 + \frac{1}{2}\sigma_z^2(q)} - q. \tag{12}$$

The best choice $\bar{q}$ then becomes that value of q which maximizes $\bar{H}(q)$. This will generally be the "Bayes equivalent"

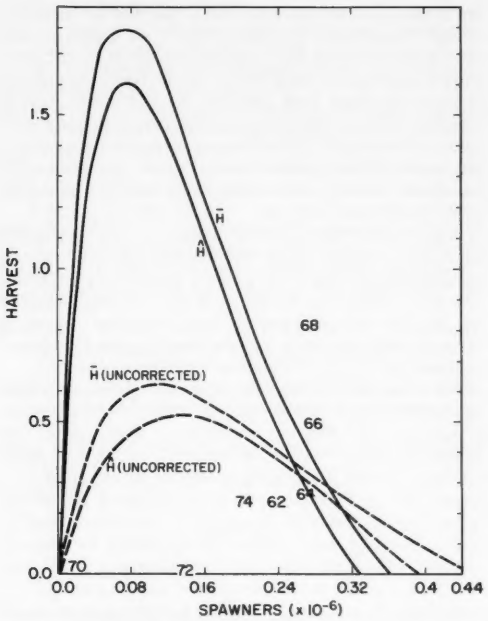

FIG. 5. Projected harvest at equilibrium versus the number of spawners, under four sets of assumptions for pink salmon from the Chignik River, Alaska.

optimal policy as defined by Mendelssohn (1980). The form of (12) is more complicated than (11), in view of (8).

Figure 5 shows $\hat{H}$ and $\bar{H}$ as functionsof q, where the parameters are estimated for data from Chignik River pink salmon. In this case, the parameter uncertainty makes little difference in either the best choice of q, or the yield at equilibrium. $\hat{H}$ (no error correction) uses the Ricker stock–recruitment relation, where the parameters are estimated by a linear regression using uncorrected observation. $\bar{H}$ (no error correction) takes the uncertainty in the estimated parameters into account. The stock–recruitment relation was averaged over the posterior distribution of parameter values. The curves labeled $\hat{H}$ and $\bar{H}$ were obtained by a similar process, where the variance of the observation error was set equal to the variance of the year-to-year fluctuation in recruitment ($\lambda = 1$). The parameters as estimated indicate extreme density dependence. Although there is a great variation in the harvest curves, the suggested optimal number of spawners differ only slightly.

Figure 6 shows a case where $\hat{H}$ has a local maximum, but $\bar{H}$ does not. If observation errors are neglected, then a rather low number of spawners appears to be optimal. However, if observation errors are accounted for, then the optimal number of spawners increases by a factor of three. If the effect of parameter uncertainty is also included, then there is no optimum level of spawners; then the indication is that the number of spawners should be increased as much as possible, until density dependence is apparent. Most pink salmon data lead

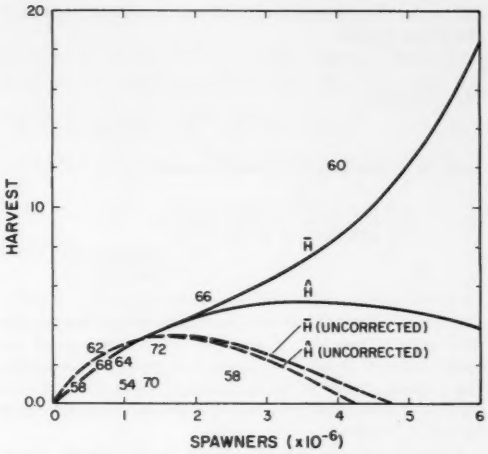

FIG. 6. Projected harvest curves as in Fig. 5, for pink salmon of the Atnarko River, B.C.

to curves resembling those of Fig. 6, rather than Fig. 5. The parameter uncertainty is so large that density-dependent effects are overwhelmed. The implication for management in this case is that escapements should be raised, to explore the possibility of large returns. One should not assign great precision to the values computed for $\hat{H}$ and $\bar{H}$. However, the qualitative difference between Fig. 5 and 6 is significant.

The determination of the spawning quota by examination of $\bar{H}$ is easy to make, but it is not easily justified on the basis of our assumptions. More elaborate schemes to determine q are examined in Ludwig and Walters (1981). These more complicated methods indicate that uncertainty in parameters is even more important than suggested by consideration of $\hat{H}$ and $\bar{H}$.

Uncertainty About the Basic Model

The preceding discussion has been based upon the assumption that the Ricker model is adequate to describe stock and recruitment. This assumption may be tested by carrying out an analogous procedure for other models of stock and recruitment. Two additional models are considered in the Appendix. Relative credibility can be assigned to the various models from the ratio of their likelihoods.

If (5) is substituted into (4) and the maximum-likelihood estimates of the parameters are chosen, then the log-likelihood of the Ricker model is given by

$$L^*_{\text{Ricker}} = -\frac{n-2}{2} - (n+1)\ln\lambda - (2n+1)\ln\sigma_u \quad \text{(Ricker)}. \tag{14}$$

Similar formulas hold for the power model,

$$L^*_{\text{power}} = -\frac{n-2}{2} - (n+1)\ln\lambda - (2n+1)\ln\sigma_u \quad \text{(power)}, \tag{15}$$

and for the three-parameter model that combines the Ricker and power models:

$$(16)\quad L^{*}_{\text{general}} = -\frac{n-3}{2} - (n+1)\ln\lambda - (2n+1)\ln\sigma_u\ (\text{general}).$$

Suppose we calculate the likelihood ratio

$$(17)\quad \frac{\text{log likelihood of Ricker model}}{\text{log likelihood of power model}} = \left[\frac{\sigma_u(\text{power})}{\sigma_u(\text{Ricker})}\right]^{2n+1}$$

The model which produces the better fit will have the smaller value of σ_u. Then (17) is a quantitative expression of the degree of belief in the models which is inspired by the data. The eventual choice of the escapement quota can be based upon a suitable compromise between the values suggested by the various models.

A more elaborate approach would be to estimate Bayes posterior probabilities for the models, using the formulation developed by Wood (1974), then compute a Bayes equivalent policy by the procedure suggested in Mendelssohn (1980). It is not possible as yet to estimate numerically the optimal, long-term, adaptive policy (Walters 1981) for the problem, since the Bayes probabilities are not a complete description of the "information state" regarding each model.

Discussion

We have applied the procedures outlined above to various data sets on British Columbian and Alaskan Pacific salmon, for a range of assumptions about measurement errors. A common result is the pathological situation illustrated in Fig. 6: the optimum spawning stock cannot be established with any confidence, and it would be best (in the sense of maximizing expected harvests) to allow much higher or at least more variable escapements. This result is especially discouraging since salmon are supposed to be more manageable than many other fishes because spawning stocks can be enumerated directly. Perhaps we are naive to draw such conclusions from simple recruitment models, or have simply been too pessimistic about the magnitude of measurement errors.

It is worth questioning the wisdom of trying to fit simple models to the data, rather than multivariate models that account for various environmental influences on recruitment. Since recruitment appears so variable with respect to spawners in most fishes, it has even been suggested that the spawner–recruit relationship should be ignored entirely. We have argued (Walters and Ludwig 1981) that appearances can be deceptive, but there is a more fundamental reason to pursue the relationship no matter how variable it may be: spawning stock decisions represent a basic connection between present and future yields. To presume that the spawner–recruit relationship is meaningless is to pretend that today's harvest decision has no influence on the recruitment future of the fishery. In this long-term view of management, it is simply irrelevant to comment that recruitment can often be predicted more accurately from environmental factors than from spawning stock; it is the spawning stock that can be controlled through management decisions. Suppose we could construct and validate a model that "explained" the stochastic deviations u_j in terms of various environmental factors; to make an optimum spawning stock decision, we would then have to hypothesize future values or probability distributions for these factors. In most cases the resulting distributions for u_{j+1}, u_{j+2}, etc. would be hardly more credible than the distribution that we estimate directly from the past data without even asking what factors were involved.

It may also be that the mean spawner–recruit relationship has a more complex shape than can be captured by simple equations like the Ricker curve (Ward and Larkin 1964, Peterman 1977). Data are generally too poor to say anything about this problem, though there are sound biological reasons to expect complex responses (i.e. depensatory mortality effects, Peterman and Gatto 1978) at low spawning stocks.

We mentioned the importance of testing the estimation procedure for small sample sizes ($10 \leq n \leq 20$). Our concern is not that larger data sets are rarely available; rather, we suspect that stock–recruit "parameters" may not be stable for longer periods. Even in the absence of persistent environmental trends, we should expect to see changes in the internal characteristics (genetic composition, local spatial structure) of stocks. Some of these effects can be tracked by adaptive parameter estimation even if they cannot be predicted, provided the estimation has a relatively short data "memory."

We have not been able to establish satisfactory estimates of measurement error variance for any of the Pacific salmon data sets. We have heard scattered reports of instances where the usual counting procedure (fishery officer count, aerial surveys, etc.) was compared to some more accurate enumeration, with results differing by as much as 200%. In some cases the recording procedure alone (by abundance intervals rather than actual counts) has probably generated errors sufficient to make $\lambda \approx 1.0$ (eq. 3).

It may be worthwhile to invest in more accurate counting procedures, at least for some key index stocks. An alternative "investment" would be to increase the variability of spawning stocks. But it is more critical now to obtain estimates of the measurement error variance (or λ of eq. 3). Otherwise a great deal of recent historical data is going to remain less than useless until it becomes irrelevant for management purposes due to possible changes in underlying stock characteristics.

Acknowledgments

We thank Jim Zidek for help with the statistical analysis, and to Randall Peterman for providing many test data sets in readily usable form.

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Appendix

Correction for Observation Errors

This Appendix describes a method for correcting observation errors, using maximum likelihood estimation. Details will be given for three models of stock and recruitment. Motivation and interpretation of these results are given in the body of the paper. Otherwise, this Appendix is self-contained.

LINEAR REGRESSION: THREE MODELS OF STOCK AND RECRUITMENT

We shall be concerned with linear models of the form

$$(1.1) \quad y_i = \sum_{p=1}^{m} x_{ip} a_p - u_i, \; 1, \ldots, n.$$

Here y_i and x_{ip} are determined from the observations. Specific examples are given below. The parameters of the model are $a_1, \ldots, a_m$, and the u_i are assumed to be independent, normally distributed, random variables, with mean 0 and variance σ_u^2. Our procedure can be extended to models where the parameters appear nonlinearly, but the estimation is more straightforward in the linear case.

Model a: the Ricker model — As in equation (1), let r_i denote the number of recruits in generation i, and let s_{i-1} denote the number of spawners in the previous generation. The Ricker model assumes that

$$(1.2a) \quad r_i = s_{i-1} \exp(a_1 + a_2 s_{i-1} - u_i), \; i = 1, \ldots, n.$$

After taking logarithms of both sides of (1.2a), we obtain the form (1.1, where $m = 2$ and

$$(1.3a) \quad y_i = \ln(r_i/s_{i-1}),$$

$$(1.4a) \quad (x_{i1}, x_{i2}) = (1, s_{i-1}).$$

Model b: the power model — With r_i and s_{i-1} defined as above, the power model assumes that

$$(1.2b) \quad r_i = s_{i-1}^{a_2} \exp(a_1 - u_i), \; i = 1, \ldots, n.$$

This results in the form (1.1), where $m = 2$ and

$$(1.3b) \quad y_i = \ln r_i,$$

$$(1.4b) \quad (x_{i1}, x_{i2}) = (1, \ln s_{i-1}).$$

Model c: the generalized Ricker model — The two preceding models may be combined in the form

$$(1.2c) \quad r_i = s_{i-1}^{a_3} \exp(a_1 + a_2 s_{i-1} - u_i).$$

In this case $m = 3$, and

$$(1.3c) \quad y_i = \ln r_i,$$

$$(1.4c) \quad (x_{i1}, x_{i2}, x_{i3}) = (1, s_{i-1}, \ln s_{i-1}).$$

MAXIMUM LIKELIHOOD AND THE METHOD OF WEIGHTED LEAST SQUARES

We shall ignore observation errors for the moment, to present the method of weighted least squares in its simplest form. Since u_i are normally distributed, the likelihood of the observations is given by

$$(1.5) \quad L = \exp\left[-\frac{1}{2\sigma_u^2} \sum_{i=1}^{n} w_i u_i^2 - \ln \sigma_u \sum_{i=1}^{n} w_i\right],$$

where u_i ($i = 1, \ldots, n$) are obtained from equation (1.1). The quantities $w_1, \ldots, w_n$ are weights which are attached to the observations. It may happen that early observations are less reliable than later ones, or the parameters of the model may have changed since the early years. Instead of disregarding early observations or anecdotal evidence, they may be assigned weights which are less than one. This modification of the procedure as described in the text is easy to make, and it promotes better use of the available information.

To estimate the parameters $a_1, \ldots, a_m$, we maximize L as a function of them. This is equivalent to minimizing the sum of squares

$$(1.6) \quad M(a) = \frac{1}{2} \sum_{i=1}^{n} w_i u_i^2.$$

At the minimizing value $\hat{a}_p$, $p = 1, \ldots, m$, we must have

$$(1.7) \quad \frac{\partial M}{\partial a_p} = \sum_{i=1}^{n} w_i u_i x_{ip} = 0, \; p = 1, \ldots, m.$$

In view of (1.1), (1.7) takes the form

$$(1.8) \quad \sum_{q=1}^{m} M_{pq} \hat{a}_q = \sum_{i=1}^{n} w_i y_i x_{ip}, \; p = 1, \ldots, m$$

where the information matrix (M_{pq}) is given by

$$(1.9)\quad M_{pq} = \frac{\partial^2 M}{\partial a_p\, \partial a_q} = \sum_{i=1}^{n} w_i x_{ip} x_{iq}.$$

THE FORM OF OBSERVATION ERRORS

One cannot correct for observation errors without some assumptions about the way in which they appear. In the present case, we assume that the actual numbers of recruits and spawners cannot be observed. The observations will be denoted by R_i and S_i, respectively. Moreover, we shall assume that the same relative error appears in both spawners and recruits:

$$(1.10)\quad R_i = r_i\, e^{v_i},\ S_i = s_i\, e^{v_i},\ i = 0, \ldots, n,$$

where v_i, $i = 0, \ldots, n$ are assumed to be independent, normally distributed, random variables, with mean zero and variance σ_v^2.

The form (1.1) still holds, but x_{ip} *and* y_i are not observable. In terms of observable variables, (1.2a) implies that

$$(1.11a)\quad u_i = a_1 + a_2 S_{i-1}\, e^{-v_{i-1}} - \ln (R_i/S_{i-1}) - v_{i-1} + v_i.$$

Similarly, (1.2b) and (1.2c) imply that

$$(1.11b)\quad u_i = a_1 + a_2 \ln S_{i-1} - a_2\, v_{i-1} - \ln R_i + v_i,$$

$$(1.11c)\quad u_i = a_1 + a_2\, S_{i-1}\, e^{-v_{i-1}} + a_3 \ln S_{i-1} - a_3\, v_{i-1} - \ln R_i + v_i.$$

Many other assumptions could be accomodated within the scheme presented below. A common feature of the models treated here is that u_i depends only upon v_i, v_{i-1}, and the model parameters. This restriction could be dropped, but it would complicate the calculation of $v_0, \ldots, v_n$ below.

MAXIMUM LIKELIHOOD ESTIMATION OF THE OBSERVATION ERRORS

In view of the presence of v_i in (1.11), the likelihood (1.5) must be modified to

$$(1.12)\quad L(a,v) = \exp\left[- \frac{M(a,v)}{\sigma_u^2} - \sum_{i=1}^{n} w_i \ln \sigma_u - \sum_{i=0}^{n} w_{i+1} \ln \sigma_v \right]$$

where

$$(1.13)\quad M(a,v) = \frac{1}{2} \sum_{i=1}^{n} w_i u_i^2 + \frac{1}{2\lambda} \sum_{i=0}^{n} w_{i+1} v_i^2.$$

The parameter λ is given by (3). As is explained there, λ must be prescribed to estimate the parameters and observation errors.

The parameters $a_1, \ldots, a_m$ and the errors $v_0, \ldots, v_n$ will be estimated by maximizing the likelihood, i.e. by minimizing $M(a,v)$. The minimizing values $\hat{a}$ and $\hat{v}$ must satisfy

$$(1.14)\quad \frac{\partial M}{\partial v_j}(\hat{a},\hat{v}) = \sum_{i=1}^{n} w_i\, \hat{u}_i\, \frac{\partial \hat{u}_i}{\partial v_j} + \frac{1}{\lambda} w_{j+1}\, \hat{v}_j = 0, \quad j = 0, \ldots, n,$$

$$(1.15)\quad \frac{\partial M}{\partial a_p}(\hat{a},\hat{v}) = \sum_{i=1}^{n} w_i\, \hat{u}_i\, \hat{x}_{ip} = 0,\ p = 1, \ldots, m.$$

$$(1.16)\quad \frac{\partial M}{\partial v_j}(\hat{a},\hat{v}) = w_{j+1}\left[\hat{u}_{j+1}\, \frac{\partial \hat{u}_{j+1}}{\partial v_j} + \frac{1}{\lambda} v_j \right] + w_j\, u_j\, \frac{\partial \hat{u}_j}{\partial v_j} = 0.$$

In particular, from (1.11) we obtain

$$(1.17a)\quad \frac{\partial u_{j+1}}{\partial v_j} = -1 - a_2\, s_j,\ \frac{\partial u_j}{\partial v_j} = +1.$$

$$(1.17b)\quad \frac{\partial u_{j+1}}{\partial v_j} = -a_2,\ \frac{\partial u_j}{\partial v_j} = 1.$$

$$(1.17c)\quad \frac{\partial u_{j+1}}{\partial v_j} = -a_2\, s_j - a_3,\ \frac{\partial u_j}{\partial v_j} = 1.$$

In each case, $\dfrac{\partial u_i}{\partial v_k} = 0$ unless $k = j$ or $k = j - 1$.

NEWTON'S METHOD

Since the system (1.15)−(1.16) is nonlinear, we shall solve it by an iterative method. Suppose that we have an initial guess a^0, v^0. Then we write

$$(1.18)\quad \begin{cases} a_p = a_p^0 + \delta a_p,\ p = 1, \ldots, m, \\ v_j = v_j^0 + \delta v_j,\ j = 0, 1, \ldots, n, \end{cases}$$

and we attempt to satisfy the equations

$$(1.19)\quad \frac{\partial M}{\partial v_j}(a^0 + \delta a,\ v^0 + \delta v) = 0,\ j = 0, \ldots, n,$$

$$(1.20)\quad \frac{\partial M}{\partial a_p}(a^0 + \delta a,\ v^0 + \delta v) = 0,\ p = 1, \ldots, m.$$

If equations (1.19) and (1.20) are expanded by Taylor's theorem, and quadratic and higher powers of δa and δv are neglected, the result is the approximate system

$$(1.21)\quad \frac{\partial M}{\partial v_j}(a^0,v^0) + \sum_{k=0}^{n} \frac{\partial^2 M}{\partial v_j \partial v_k}(a^0,v^0)\, \delta v_k + \sum_{q=1}^{m} \frac{\partial^2 M(a^0,v^0)}{\partial v_j \partial a_q}\, \delta a_q = 0,\ j = 0, \ldots, n,$$

$$(1.22)\quad \frac{\partial M}{\partial a_p}(a^0,v^0) + \sum_{k=0}^{n} \frac{\partial^2 M}{\partial v_j \partial v_k}(a^0,v^0)\, \delta v_k + \sum_{q=1}^{m} \frac{\partial^2 M\,(a^0,v^0)}{\partial a_p \partial a_q}\, \delta a_q = 0,\ p = 1, \ldots, m.$$

The system (1.21)−(1.22) is linear in δv and δa; the method of solution is given below. Then the next approximation v^1, a^1 is obtained from (1.18). Since the system (1.21)−(1.22) is only an approximation, v^1 and a^1 may still not satisfy (11.19) and (1.20) to sufficient accuracy. If not, further approximations v^2, a^2, etc. may be obtained by repeating the procedure described above. If the initial guess is sufficiently accurate, the number of significant figures doubles with each iteration. Thus, success in applying Newton's method depends upon obtaining an accurate first guess a^0, v^0.

A good initial guess may be obtained by varying the parameter λ. If $\lambda = 0$, then no corrections are made to the observations, and $v_i = 0$, $i = 0, \ldots, n$. Then δa_p, $p = 1, \ldots, m$ may be obtained by solving (1.22) with $a_p^0 = 0$, $p = 1, \ldots, m$, which is equivalent to (1.8). Now we may choose a small value of λ, and use $v_i^0 = 0$, $i = 0, \ldots, n$, and $a_p^0 = \delta a_p$, $p = 1, \ldots, m$. If λ is small enough, the subsequent iterations must converge. Then we may increase λ slightly, and iterate again to obtain v and a.

Some computing time is saved if the initial guess is made by extrapolation in λ. Suppose that we have a solution of (1.15)−(1.16) for some value of λ:

$$(1.23)\quad \frac{\partial M}{\partial v_j}(a(\lambda), v(\lambda), \lambda) = 0,\ j = 0, \ldots, n,$$

$$(1.24)\quad \frac{\partial M}{\partial a_p}(a(\lambda), v(\lambda), \lambda) = 0,\ p = 1, \ldots, m.$$

If (1.23) and (1.24) are differentiated with respect to λ, the result is

$$(1.25)\quad \frac{\partial^2 M}{\partial v_j \partial \lambda} + \sum_{k=0}^{n} \frac{\partial^2 M}{\partial v_j \partial v_k}\frac{\partial v_k}{\partial \lambda} + \sum_{q=1}^{m} \frac{\partial^2 M}{\partial v_j \partial a_q}\frac{\partial a_q}{\partial \lambda} = 0,$$

$$j = 0, \ldots, n,$$

$$(1.26)\quad \frac{\partial^2 M}{\partial a_p \partial \lambda} + \sum_{k=0}^{n} \frac{\partial^2 M}{\partial a_p \partial v_k}\frac{\partial v_k}{\partial \lambda} + \sum_{q=1}^{m} \frac{\partial^2 M}{\partial a_p \partial a_q}\frac{\partial a_q}{\partial \lambda} = 0,$$

$$p = 1, \ldots, m.$$

This system has the same form as (1.21)–(1.22), and it may be solved in the same way. The only difference is in first term in each equation. These terms are obtained from (1.15)−(1.16):

$$(1.27)\quad \frac{\partial^2 M}{\partial v_j \partial \lambda} = -\frac{1}{\lambda^2} w_{j+1} v_j,\ j = 0, \ldots, n.$$

$$(1.28)\quad \frac{\partial^2 M}{\partial a_p \partial \lambda} = 0,\ p = 1, \ldots, m.$$

If the solutions of (1.23)−(1.26) are known for $\lambda = \lambda_0$, then an initial guess for $\lambda = \lambda_1$ is given by

$$(1.29)\quad v_j^0(\lambda_1) = v_j(\lambda_0) + (\lambda_1 - \lambda_0)\frac{\partial v_j}{\partial \lambda}(\lambda_0),\ j = 0, \ldots, n,$$

$$(1.30)\quad a_p^0(\lambda_1) = a_p(\lambda_0) + (\lambda_1 - \lambda_0)\frac{\partial a_p}{\partial \lambda}(\lambda_0),\ p = 1, \ldots, m.$$

This procedure will lead to convergent Newton iterations if $\lambda_1 - \lambda_0$ is small enough. The combined Newton's method and extrapolation can fail only if successive increments in λ must be taken smaller and smaller. This situation is explained below.

Calculation of the Observation Errors

Now we turn to the solution of (1.21). Assume for the moment that δa_p, $p = 1, \ldots, m$ are known. We define g_k, $k = 0, \ldots, n$ and h_{pk}, $p = 1, \ldots, m$; $k = 0, \ldots, n$ as the solutions of the systems

$$(1.31)\quad \sum_{k=0}^{n} \frac{\partial^2 M}{\partial v_j \partial v_k}(a^0, v^0) g_k = \frac{\partial M}{\partial v_j}(a^0, v^0),\ j = 0, \ldots, n,$$

$$(1.32)\quad \sum \frac{\partial^2 M}{\partial v_j \partial v_k}(a^0, v^0)\, h_{pk} = \frac{\partial^2 M(a^0, v^0)}{\partial a_p \partial v_j}$$

$$j = 0, \ldots, n;\ p = 1, \ldots, m.$$

Since the system (1.21) is linear in δv, we obtain

$$(1.33)\quad \delta v_j = -g_j - \sum_{p=1}^{m} h_{pj}\, \delta a_p.$$

Now we evaluate the coefficient matrix in (1.31) and (1.32). It follows from differentiating (1.16) that

$$(1.34)\quad \frac{\partial^2 M}{\partial v_j \partial v_k} = w_{j+1}\left[\frac{\partial u_{j+1}}{\partial v_j}\frac{\partial u_{j+1}}{\partial v_k} + u_{j+1}\frac{\partial^2 u_{j+1}}{\partial v_j \partial v_k} + \frac{\delta^{jk}}{\lambda}\right] + w_j \frac{\partial u_j}{\partial v_j}\frac{\partial u_j}{\partial v_k},$$

where $\delta^{jk} = 0$ if $j \neq k$, and $\delta^{jj} = 1$. The first derivatives which appear in (1.34) are given by (1.17), and the second derivatives are obtained by differentiating those equations. Thus for each of the three models we have, respectively,

$$(1.35a)\quad \frac{\partial^2 u_{j+1}}{\partial v_j \partial v_j} = a_2 s_j,\ \frac{\partial^2 u_j}{\partial v_j \partial v_j} = 0,\ \text{if } j = 0, \ldots, n.$$

$$(1.35b)\quad \frac{\partial^2 u_i}{\partial v_j \partial v_j} = 0 \text{ for all } i, j, k.$$

$$(1.35c)\quad \frac{\partial^2 u_{j+1}}{\partial v_j \partial v_j} = a_2 s_j,\ \frac{\partial^2 u_j}{\partial v_j \partial v_j} = 0,\ \text{if } j = 0, \ldots, n.$$

In every case,

$$(1.36)\quad \frac{\partial^2 u_i}{\partial v_j \partial v_k} = 0 \text{ where } j = k, \text{ and unless } i = j + 1 \text{ or } i = j.$$

The relations (1.17) and (1.36) imply that only the diagonal terms and those adjacent to the diagonal are different from zero in $\left(\frac{\partial^2 M}{\partial v_j \partial v_k}\right)$. In particular, (1.34) takes the form

$$(1.37)\quad \frac{\partial^2 M}{\partial v_j \partial v_j} = w_{j+1}\left[\left(\frac{\partial u_{j+1}}{\partial v_j}\right)^2 + u_{j+1}\frac{\partial^2 u_{j+1}}{\partial v_j^2} + \frac{1}{\lambda}\right] + w_j\left(\frac{\partial u_j}{\partial v_j}\right)^2, \; j = 0, \ldots, n,$$

$$(1.38)\quad \frac{\partial^2 M}{\partial v_j \partial v_{j+1}} = \frac{\partial^2 M}{\partial v_{j+1}\partial v_j} = w_{j+1}\frac{\partial u_{j+1}}{\partial v_{j+1}}\frac{\partial u_{j+1}}{\partial v_j}, \quad j = 0, \ldots, n.$$

All of the remaining elements of $\left(\frac{\partial^2 M}{\partial v_j \partial v_k}\right)$ are zero. Systems which have such a "tri-diagonal" form are important in numerical analysis. Efficient solution subroutines are available at most large computer installations. The number of operations necessary to solve such a system is proportional to the first power of $n + 1$, rather than a higher power.

Calculation of the Parameter Estimates

After g_k and h_{pk} have been calculated, the form (1.33) may be substituted into (1.22). The result is

$$(1.39)\quad \left(\frac{\partial M}{\partial a_p} - \sum_{k=0}^{n}\frac{\partial^2 M}{\partial a_p \partial v_k} g_k\right) + \sum_{q=1}^{m}\left(\frac{\partial^2 M}{\partial a_p \partial a_q} - \sum_{k=1}^{n}\frac{\partial^2 M}{\partial a_q \partial v_k} h_{qk}\right)\delta a_q = 0,$$

The system (1.39) is a corrected form of the ordinary regression equations (1.8). The corrected information matrix (M'_{pq}) is given by

$$(1.40)\quad M'_{pq} = \frac{\partial^2 M}{\partial a_p \partial a_q} - \sum_{k=0}^{n}\frac{\partial^2 M}{\partial v_k \partial a_p} h_{qk}.$$

Since the additional parameters $v_0, \ldots, v_n$ must be estimated, the corrected matrix (M'_{pq}) corresponds to less information that was expressed in (M_{pq}). If the variance ratio λ becomes too large, the matrix (M'_{pq}) may become singular, or no longer positive-definite. In such a case, there is no longer enough information to produce any estimate of the parameter. As this situation is approached, the increments in λ which produce convergent Newton iterations become smaller and smaller. The lack of information is also reflected in the increasing size of confidence regions for the parameters, as will be shown below.

The maximum likelihood estimate for σ_u is obtained by differentiating (1.12) as a function of σ_u, holding λ fixed. The result is

$$(1.41)\quad \hat{\sigma}_u^2 = \frac{2M(\hat{a},\hat{v})}{\sum_{i=1}^{n} w_i + \sum_{i=0}^{n} w_i}.$$

The numerator in (1.41) is just the residual sum of squares. To correct the bias in this estimate, we may set

$$(1.42)\quad \tilde{\sigma}_u^2 = \frac{2M(\hat{a},\hat{v})}{n - p}.$$

A more refined Bayesian approach would be to treat σ_u^2 like the other parameters, and work with their joint posterior distribution. The present, cruder procedure seems to be adequate to deal with fisheries data.

Uncertainty in the Parameter Estimates

To assess the precision in our estimates $\hat{a}$, we return to (1.13), and we determine v_j as functions of a_p from (1.14):

$$(1.43)\quad \frac{\partial M}{\partial v_j}(a, v(a)) = 0, \; j = 0, \ldots, n.$$

If (1.43) is differentiated with repect to a_p, the result is

$$(1.44)\quad \frac{\partial^2 M}{\partial a_p \partial v_j} + \sum_{k=0}^{n}\frac{\partial^2 M}{\partial v_j \partial v_k}\frac{\partial v_k}{\partial a_p} = 0, \; p = 1, \ldots, m.$$

By comparing (1.44) and (1.32), we see that, at $\hat{a}$, $\hat{v}$,

$$(1.45)\quad \frac{\partial v_k}{\partial a_p} = -h_{pk}, \; p = 1, \ldots, m; \; k = 0, \ldots, n.$$

Furthermore, the total second derivatives of M are given by (compare (1.40))

$$(1.46)\quad \frac{\partial^2 M(a, v(a))}{\partial a_p \partial a_q} = \frac{\partial^2 M}{\partial a_p \partial a_q} + \sum_{k=0}^{n}\frac{\partial^2 M}{\partial a_p \partial v_k}\frac{\partial v_k}{\partial a_q} = M'_{pq}.$$

Since the first derivatives of M are zero at $\hat{a}$, $\hat{v}$, we obtain the approximate form

$$(1.47)\quad M(a, v(a)) \sim M(\hat{a},\hat{v}) + \frac{1}{2}\sum_{p,q=1}^{m} M'_{pq}(a_p - \hat{a}_p)(a_q - \hat{a}_q).$$

Then if we fix $\sigma_u = \tilde{\sigma}_u$ and set $v = v(a)$, the likelihood takes the form (6). When considered as a function of a, the likelihood is proportional to a multivariate normal density, with mean $\hat{a}$, and with a covariance matrix given by (9).

A General Approach to the Culture of Planktonic Rotifers[1,2]

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STEMBERGER, R. S. 1981. A general approach to the culture of planktonic rotifers. Can. J. Fish. Aquat. Sci. 38: 721–724.

A general method for establishing cultures of planktonic rotifers from natural waters is described. Algal isolates are tested for their suitability as food for rotifers collected from the same source and season. Rotifer clones displaying the highest reproductive rates under the given culture conditions are selected for the final culture system. This procedure yielded indefinite cultures for the eulimnetic species, *Asplanchna priodonta, A. herricki, Polyarthra major*, and *Synchaeta pectinata*, and appears to have a good probability of success when the diet of a species is unknown. Algal isolates from the same source as the rotifers produced better results than algae obtained from commercial sources. Cryptomonad species produced the most consistent positive responses in growth and reproduction of rotifers tested.

Key words: rotifers, zooplankton culture, *Asplanchna, Polyarthra, Synchaeta, Cryptomonas*

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On trouvera dans l'article qui suit une méthode générale de cullture de rotifères planctoniques provenant d'eaux naturelles. Il faut s'assurer que les isolats d'algues conviennent bien comme nourriture des rotifères recueillis au même endroit et dans la même saison. Les clones de rotifères dont le taux de reproduction est le plus élevé dans des conditions données de culture seront choisis pour le système de culture final. Grâce à cette méthode, on a obtenu des cultures indéfinies des espèces eulimnétiques *Asplanchna priodonta, A. herricki, Polyarthra major* et *Synchaeta pectinata*, et les chances de succès semblent très bonnes, même si le régime d'une espèce est inconnu. Les isolats d'algues provenant de la même source que les rotifères donnèrent de meilleurs résultats que les algues provenant de sources commerciales. Parmi les rotifères testés, les espèces de cryptomonades eurent les réponses positives de croissance et de reproduction les plus uniformes.

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ROTIFERS are a predominant group of freshwater zooplankton and may form important links in pelagic food webs as prey for crustacean predators (McQueen 1969; Gilbert and Williamson 1978; Li and Li 1979), as first food for larval fish (Siefert 1972) and in nutrient cycling (Makarewicz and Likens 1979). Rotifers have been used in bioassay studies (Buikema et al. 1974; Beeton et al. 1976), aging studies (Meadow and Barrows 1971), and for rearing fish larvae (Theilacker and McMaster 1971; Howell 1979). However, because their role in pelagic ecosystems is poorly known, rotifers have been omitted from most lake ecosystem models (Scavia 1979). Quantitative information on rate processes and food web relationships require laboratory cultures of pelagic species which have seldom been available to experimentalists.

Although laboratory culture methods for a variety of freshwater littoral and benthic rotifers have been reported (see reviews Gilbert 1970; Campbell et al. 1973; Pourriot 1977), few techniques are completely defined and even fewer techniques exist for planktonic species (Pourriot 1965; Gilbert 1968, 1970).

Many rotifer culture techniques have used algal food sources belonging to the Chlorophycophyta and Eugleno-

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phycophyta such as *Chlamydomonas*, *Chlorella*, and *Euglena*. These food resources have the advantage of being available from culture collections and are suitable for some benthic and littoral species such as *Brachionus* and *Euchlanis*. However, such algae appear to have limited dietary value to most true planktonic species which are apparently more specialized for food quality (Pourriot 1977).

A variety of planktonic rotifers can be grown for relatively long periods of time by keeping them in their native lake water (Makarewicz and Likens 1979; Stemberger et al. 1979). A logical extension of this for establishing cultures of pelagic algivorous species is to isolate algae and rotifers from the same source at a time when rotifer populations are actively reproducing. By testing the algal isolates for their suitability to support rotifer reproduction and population growth in the laboratory, one can greatly increase the probability of finding a compatible combination that will yield indefinite culture.

From the practical standpoint, methods for zooplankton culture should be simple. Therefore, a unialgal food source is preferable to a mixed culture. The algae should be motile so that they remain in suspension without artifical mixing. The medium should serve both algae and rotifers, and the volume of the zooplankton cultures should be sufficiently large to minimize the need to renew the medium or thin the population.

In this paper a defined method for establishing planktonic rotifers in culture with specific reference to cultures of *Asplanchna priodonta*, *A. herricki*, *Synchaeta pectinata*, *S. oblonga*, and *Polyarthra major* is reported.

Materials and methods — Guillard's Woods Hole MBL medium (Nichols 1973) = WC medium (Guillard 1975) was modified for algae and rotifer cultures by reducing K_2HPO_4 and $NaNO_3$ concentration to half, which improved growth of microflagellates. Boron as H_3BO_3 was added to yield 1.3×10^{-4} g/L and TRIS buffer was eliminated as a modification suggested by Guillard 1975. For algal cultures, the medium was sterilized by filtration through a 0.22-μm Millipore filter. Nonsterile medium was used for culturing rotifers during routine maintenance.

Water samples were collected from 2 m below the surface of Douglas Lake, Pellston, Michigan, and Lake Michigan in the spring just before and during the spring rotifer bloom. Diatoms were isolated from unfiltered lake water using a sterile pipette technique (Guillard 1973). Flagellated algae were isolated by the following technique after the lake water sample was filtered through 25 μm mesh Nitex screen: filtered lake water was enriched with 10% modified WC and placed in a growth chamber at 20°C and 6500 lx of continuous light provided by cool-white fluorescent bulbs. After 3 d of incubation, 50 μL (one drop) of the enriched culture was inoculated into 5-mL glass vials containing 2 mL full strength medium. After several days, the vials were viewed in vitro through a dissecting microscope with light reflected from a polished substage mirror which provided adequate contrast to discern moving particles as small as 2 μm at 50× magnification. A series of subcultures was made from vials with microflagellate growth until unialgal xenic cultures were obtained. The unialgal cultures were maintained in Erlenmeyer flasks with aluminum foil covers in growth chambers at 20°C and 4300 lx of cool-white fluorescent lighting on a 14:10 light dark (LD) cycle.

A few microflagellates were purchased from the Culture Centre of Algae and Protozoa, the University of Cambridge, and the University of Texas Starr Collection.

Isolation and cultivation of rotifers — Rotifers were collected with a 20-mesh plankton net from Douglas Lake and Lake Michigan ~3 wk after algae were initially isolated. Rotifers were kept in 28 × 35 mm Stender dishes and fed cultured microflagellates and diatoms at final densities between 5000 and 10 000 cells/mL and 2000 and 4000 cells/mL, respectively. Five to 10 rotifers of one species were serially washed with sterile medium in a spot depression plate before adding to the Stender dish. Medium and algae in the Stender dishes were changed every 3 d. Egg development, reproduction, and gut contents were examined daily. Algal species producing marginal growth and reproduction in the rotifers were combined and again fed to the rotifers to see if reproduction and survivorship improved with a mixed diet. Rotifers were handled with a disposable Pasteur pipette connected to latex tubing fitted with a mouthpiece, and transfers were made under a dissecting microscope. Trial feedings were performed at 16–20°C and 500–6500 lx of cool-white fluorescent lights on a 14:10 LD cycle. Rotifer cultures showing the greatest population increase were isolated and the fastest growing clones were selected for further culture.

Batch rotifer cultures were maintained in 250- to 1000-mL Griffin beakers and replacement of medium was required routinely every 6–10 d. Animals were fed sparingly every 3 d, with final algal densities less than 15 000 cells/mL. The medium was changed by pouring the contents of the beaker into a sterile Nalgene bottle with an opening covered with 54 μm Nitex screen. The rotifers were concentrated and rinsed with fresh nonsterile medium, and fresh exponentially growing algae were added.

Results — Successful cultures were obtained for the planktonic species *A. priodonta*, *A. herricki*, *S. pectinata*, *S. oblonga*, and *P. major* based on the above technique. Cultures which showed little population increase but were maintained for 1 to 2 mo were *Ascomorpha ecaudis*, *Keratella crassa*, *K. cochlearis*, *Ploesoma truncatum*, and *Synchaeta stylata* (Table 1).

Among cultured algal species, *Cryptomonas erosa* var. *reflexa* was a nutritionally adequate and readily accepted food source for a number of raptorial feeding rotifers which differed greatly in body size. *Asplanchna priodonta*, *A. herricki*, *S. pectinata*, and *P. major* were successfully cultured solely on *C. erosa* v. *reflexa*. The most consistent cultures were those of *A. priodonta* which have been maintained for over 2 yr. Population densities in batch culture exceeded 15 000 ind./L. A clone of *S. pectinata* maintained for 2 yr reached population densities of 20 000 ind./L but with fluctuating populations and the occasional appearance of males. This species did equally well feeding on the smaller *Cryptomonas Ozolini*. Densities of *C. erosa* v. *reflexa* higher than 20 000 cells/mL had adverse effects on rotifer reproduction.

The highest density achieved for *P. major* cultures was 6700 ind./L. *Polyarthra* often got caught in the surface film

TABLE 1. Value of various food sources for rotifer culture. (a) High sustained reproduction for 3 or more months, (b) moderate reproduction for up to 2 mo, (c) maintenance of less than 1 mo, no reproduction, and (d) no apparent value for culture. Blank spaces indicate no data.

Rotifer isolates	*Cryptomonas erosa* var. *reflexa*	*Cryptomonas Ozolini*	*Cryptomonas ovata*	*Cryptomonas* sp.[1]	*Ochromonas danica*[1]	*Chlamydomonas reinhardii*[1]	*Chlamydomonas* sp.	*Asterionella formosa*	*Fragilaria crotonensis*	*Bodo lens*	*Synchaeta pectinata*
Ascomorpha ecaudis		b		c	d						
Asplanchna herricki	a	c		c				b	c		b
A. priodonta	a		b					b	c		c
Collotheca mutabilis	c	c									
Gastropus stylifer		c									
Keratella crassa		b				c				c	
K. cochlearis		b			d	c	d			c	
K. earlinae						c					
K. hiemalis										c	
Kellicottia longispina										c	
Ploesoma lenticulare		c									c
P. truncatum	b										c
Polyarthra euryptera	c										
P. major	a						c				
P. vulgaris		c		d	d		c			c	
Synchaeta grandis	c			c							
S. oblonga	c	c	a								
S. pectinata	a	a	c								
S. stylata	b	c									

[1]Purchased from culture collections.

of the growth medium which caused relatively high mortality. *Polyarthra major*, however, avoided the surface under continuous overhead lighting which improved survivorship in cultures. A single clone was maintained for 3 mo.

Asplanchna herricki cultures achieved densities of ~5000 ind./L. This large omnivore often formed colonies of 10–30 individuals which were connected by adhesive secretions from the base of the pedal gland. A clone of this species was maintained in culture for 1 yr. Reproduction was enhanced when the species was fed on *S. pectinata* which they voraciously consumed.

Cultures of *S. oblonga* were maintained for 2 mo at 8°C, fed with *Cryptomonas ovata*. Although densities of 10 000 ind./L were obtained, indefinite reproduction was not achieved. *Ascomorpha ecuadis*, a raptorial feeder and *K. cochlearis* and *K. crassa*, two suspension feeding species, were maintained for 2 mo on *C. Ozolini*. However, reproductive rates were very low. Two species with grasping mouth parts, *S. stylata* and *P. truncatum*, yielded only marginal reproduction and growth on *C. erosa* v. *reflexa* (Table 1).

The purchased cultures, *Chlamydomonas reinhardii*, *Cryptomonas* sp., and *Ochromonas danica*, chosen on the basis of size and motility, did not support reproduction in the rotifers tested (Table 1). It quickly became apparent that this approach had a low probability of success and it was discontinued.

No attempt was made in the above methods to develop bacteria-free cultures. If monoxenic rotifer cultures are desired, a completely sterile approach such as Gilbert's (1970) may be applied. Bacteria contamination did not present a problem in this study which was conducted at temperatures below 20°C. However, contamination of rotifer cultures arose from airborne green algae such as *Chlorella* and *Ankistrodesmus*.

Discussion — Cultures of a number of rotifer species in the present report have previously been established by other workers but methods were not totally defined or explicitly stated. Pejler (1977) reported that good growth and reproduction of *A. priodonta* were obtained using the cryptomonad *Rhodomonas minuta*. Pourriot (1965) and Pourriot and Hillbricht-Ilkowska (1969) cultured *A. priodonta*, *S. pectinata*, and *S. oblonga* on *Cryptomonas curvata*. Only *A. herricki* and *P. major* have not been previously reported in culture.

Although reproduction in *K. cochlearis* and *K. crassa* was low on *C. Ozolini*, Lindstrom and Pejler (1975) reported high sustained reproduction in *K. cochlearis* on *R. minuta*. They isolated both organisms from the same source.

I was able to establish defined culture methods for a number of planktonic species in a relatively short period of time. I attribute the success of these efforts partly to the medium which supports growth of a variety of microflagellates, but primarily to the linking of rotifers to algal isolates

taken from the same source and season. Pourriot (1977) reported that major differences in food preferences exist among populations of *Brachionus calyciflorus*. If this is a general phenomenon in rotifers, then any attempt to duplicate a defined culture method for a given species and food source may not succeed for isolates taken from different sources. For this reason, it is best to use rotifer and algal isolates from the same source. Ultimately, the achievement of indefinite cultures probably depends on selection of those rotifer genotypes which are most compatible to the particular culture environment.

The most important algae for the rotifer cultures established in this study were the cryptomonads. This group of algae deserves more attention with respect to food web pathways to rotifers and to other algivorous zooplankton. Munawar and Munawar (1975, 1978) have shown that cryptomonads are among the most important contributors to phytoplankton biomass in the Laurentian Great Lakes. It is evident from the present study and that of Pourriot (1965, 1977) that a variety of algae of suitable size may be eaten by a zooplankton species, but only a limited number of algal species will be nutritionally adequate and therefore of importance to zooplankton culture.

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Sex Reversal in Carp (*Cyprinus carpio*) by Oral Administration of Methyltestosterone

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NAGY, A., M. BERCSÉNYI, AND V. CSÁNYI. 1981. Sex reversal in carp (*Cyprinus carpio*) by oral administration of methyltestosterone. Can. J. Fish. Aquat. Sci. 38: 725–728.

Effects of oral administration of methyltestosterone on sex reversal from female to male in carp (*Cyprinus carpio*) was evaluated using all-female gynogenetic carp. Methyltestosterone supplemented in the diet at 100 μg/g for 36 d was tested at 20 and 25°C and for varying times of initiation of treatment. The treatments induced partial and more complete sex reversal at 20 and 25°C, respectively. At 20°C hermaphrodites appeared frequently. At 25°C, the most successful sex reversal occurred, particularly when methyltestosterone was administered starting 44 d and terminating 80 d after hatching.

Key words: carp, all-female carp, sex reversal, gynogenesis, methyltestosterone, androgen treatment

NAGY, A., M. BERCSÉNYI, AND V. CSÁNYI. 1981. Sex reversal in carp (*Cyprinus carpio*) by oral administration of methyltestosterone. Can. J. Fish. Aquat. Sci. 38: 725–728.

Des carpes (*Cyprinus carpio*) gynogénétiques toutes femelles ont servi à évaluer les effets de l'administration perorale de méthyltestostérone sur la réversion du sexe, de femelle à mâle, chez cette espèce. Nous avons fait des expériences avec le méthyltestostérone ajouté au régime alimentaire à une concentration de 100 μg/g pendant 36 jours à 20 et 25°C, le traitement commençant à divers moments. Le traitment provoque une réversion du sexe partielle et plus complète à 20 et à 25°C, respectivement. Des hermaphrodites apparaissent fréquemment à 20°C. La réversion du sexe a le mieux réussi à 25°C, en particulier quand le méthyltestostérone commençait à être adminstré 44 jours, et se terminait 80 jours après l'éclosion.

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DURING our work on gynogenesis in carp (*Cyprinus carpio*), which began with the aim of developing new tools in fish genetics and applying the results to practical animal breeding (Nagy et al. 1978, 1979), several all-female gynogenetic lines were established. Experiments on sex reversal were necessary to make crosses between all-female lines to produce high-yielding hybrids and also to enable mass production of monosex fish. Several well-documented cases are known of successful sex reversal in different species of fish by early androgen treatment (Schreck 1974). Most of these experiments were difficult to evaluate because the treated fish were usually genetically bisexual. But in our case the use of all-female gynogenetic carp ensured that males that appeared after hormone treatment had been sexually reversed.

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Materials and methods — Gynogenesis — The gynogenetic fry were produced by methods described by Nagy et al. (1978). In brief, sperm irradiated by a Co source (1000 Gy) was used to fertilize the eggs at 20°C. Five and/or 15 min after fertilization, the zygotes were quickly cooled down to 4°C. After 60 min at 4°C, the eggs were warmed up to 20°C.

Sex reversal — The androgen used most frequently for fish sex reversal is methyltestosterone. Administration of methyltestosterone at different concentrations has different effects. For example, it accelerated growth of goldfish (*Carassius auratus*) when incorporated in the diet at a concentration of 1 μg/g (Yamazaki 1976). At medium dosages (10–50 μg/g) a complete sex reversal from female to male was obtained in goldfish (Yamamoto and Kajishima 1968) and in tilapia (*Tilapia aurea*) (Guerrero 1973; Nakamura 1975). At high dosages (1000 μg/g) methyltestosterone exerted a paradoxical

feminizing effect on the gonad of genetic males in tilapia (Nakamura 1975) and produced androgenic castration in both sexes of medaka (*Oryzias latipes*) (Yamamoto 1958).

Sex reversal depends not only on the concentration of methyltestosterone incorporated in the diet, but on the age of the fish being treated, the duration of hormone treatment, the rearing temperature, the food, and the species studied. The wrong choice and/or setting of parameters led to numerous unsuccessful attempts (see review by Yamamoto 1969).

Experimental conditions — For experimental purposes, the duration of treatment, the concentration of methyltestosterone, and the food content were fixed, while the temperature used and the initiation time of the treatments were changed between the various groups.

Water temperatures used in Experiments I and II were 20 ± 2°C and 25 ± 1°C, respectively. During the treatments, the fish were fed a diet supplemented with methyltestosterone at a dosage of 100 μg/g ad lib. To prepare the androgen-containing diet, crystalline methyltestosterone was dissolved in 50% ethanol at 100 mg/mL and added to the food at a fixed dosage. The diet used was developed in the laboratory because the available commercial dry diets for carp culture were not complete, especially in the first month of growth. The diet formulation was:

Constituent	Quantity
Ground cattle liver	200 g
Ground cattle heart	300 g
Commercial broiler hen food	500 g
Whole eggs	2
Vitamin C	0.5 g
Vitamin E	0.5 g
Phylasol-combi (Vitamin formula)[1]	5 g

The experimental groups were raised in 160-L glass aquaria, under an artificial photoperiod of 14:00 light and 10:00 darkness with filtered and aerated water.

Experimental groups — Experiment I (water temperature 20°C) — The gynogenetic fry were divided into six groups designated A, B, C, D, E, and Q. Group Q served as the control. The remaining groups were fed diets supplemented with methyltestosterone for periods of 36 d, beginning 8, 26, 44, 62, and 80 d after hatching, respectively. Fish were fed the control diet before and after androgen treatment.

Experiment II (water temperature 25°C) — The first five groups in this experiment (F, G, H, I, and J) were treated the same as in Experiment I. Group K was fed with methyltestosterone for a period of 108 d, beginning 8 d after hatching. Group Q_2 served as the control. The remaining seven groups (L, M, N, O, P, R, and S) were treated according to the length of the animals: from 7 to 21 mm, 13 to 19 mm, 19 to 57 mm, 25 to 75 mm, 31 to 93 mm, 37 to 111 mm, and 43 to 129 mm, respectively. That is the fish were treated only when they were within the specific length category.

Sex determination — In a sample from each group the sex was determined when the fish reached 7 mo of age. Ovaries in these carp typically begin to mature at 6 mo of age. They become slightly granular in appearance, and oocytes are easily detectable with a microscope. At this age male gonads are mature and contain fertile sperm (Gupta 1975). In the experimental groups female or male phenotype was established if oocytes or moving sperm were detected, respectively. The whole gonad was sectioned and examined microscopically; in the case of undifferentiated gonads, a histological examination was made.

Results — Experiment I (water at 20°C) — In Experiment I true sex reversal occurred in all groups treated except Group A, but the presence of females and hermaphrodites showed that the treatments did not totally reverse sex at 20°C (Table 1). The highest frequency of sex-reversed males were in Groups D and E. Mortality in the treated groups was not significantly higher than that of the control group. There were no siginificant differences in the mean gonadosomatic index of males (gonad weight as a percentage of body weight) between the groups. They varied between 0.2 and 0.5%.

Experiment II (water at 25°C) — The treatments of groups F through J were the same as in Experiment I, but they had different effects. There were no females in Groups G, H, I, and K, just males and undifferentiated fry. In Group J only one sex-reversed male was found out of the five fish. The number of sexually undifferentiated animals was highest in Group K, which was treated for the longest period (108 d, Table 2).

Sex reversal was also pronounced in groups treated according to the length of the animals (Table 3). Only males were found in Group M while Groups L, N, R, and O–P contained males and undifferentiated fry. Treatment started at a length of 43 mm had no effect (Group S). Hermaphrodites did not appear at 25°C. The mortality rate was higher during these treatments than it was in Experiment I, but it was due to the increased number of animals in the groups. The mean gonadosomatic index of sex-reversed males differed greatly between the groups (Fig. 1). The most highly developed testes filling the entire body cavity were found in Group H; from each fish in this group, sperm oozed from the genital pore upon stripping of the belly.

Succesful crosses were made between six females sex-reversed into males from Experiment H and normal females. The progeny (at least 200 in each cross) were raised in ponds. In all cases the offspring were exclusively females in accordance with female homogamy in carp.

Discussion — This study demonstrates that the oral administration of methyltestosterone at 100 μg/g food induced partial or complete sex reversal from female to male in carp

[1]Produced by Phylaxia, Hungary, and contains:

Vitamin A	50 000 I.U.	D_3	10 000 I.U.
B_1	10 mg	E	100 I.U.
B_2	25 mg	K_3	10 mg
B_3	45 mg	Biotine (H)	0.5 mg
B_6	10 mg	Folic acid	0.5 mg
B_{12}	60 mg	Nicotinic acid	175 mg
C	500 mg	Dextrose	4 g

TABLE 1. Sex reversal of carp by oral administration of methyltestosterone at 20°C.

Group	A	B	C	D	E	Q
Treatment period: from fertilization (d)	8–44	26–62	44–80	62–98	80–116	Control
No. of animals: at beginning of treatment	50	50	30	30	31	30
at end of treatment	33	27	30	27	28	17
tested	12	13	22	19	10	10
Average weight (g): at beginning of treatment	0.003	0.4	1.3	3.6	6.0	0.003
at end of of treatment	1.1	2.1	4.0	9.9	15.5	17.2
Sex distribution among the animals tested in percent:						
female	91.6	38.5	36.4	26.3	20	100
hermaphrodite	8.4	38.5	13.6	10.6	0	0
male	0	15.4	45.4	63.1	70	0
undifferentiated	0	7.6	4.6	0	10	0

TABLE 2. Sex reversal of carp by oral administration of methyltestosterone at 25°C.

Group	F	G	H	I	J	K	Q_2
Treatment period: from fertilization (d)	8–44	26–62	44–80	62–98	80–116	8–116	Control
No. of animals: at beginning of treatment	100	100	58	60	40	100	100
at end of treatment	51	53	37	30	18	30	63
tested	9	7	10	15	5	8	30
Average weight (g): at beginning of treatment	0.003	0.1	1.6	1.3	3.3	0.003	0.003
at end of of treatment	0.7	1.3	3.7	7.1	11.2	18.0	19.4
Sex distribution among the animals tested in period:							
female	11.1	0	0	0	80	0	100
male	88.9	71.4	80	86.7	20	25	0
undifferentiated	0	28.6	20	13.3	0	75	0

under experimental conditions. In Experiment I the frequent appearance of hermaphrodites opens experimental possibilities, such as the production of self-fertilizable animals, as in the work of Jalabert et al. (1975) with trout. Self-fertilization would be an effective tool for rapid production of highly homozygous strains. In Experiment II, the water temperature of 25°C increased the effectiveness of the hormone treatment in most of the groups. The sensitive period, during which complete sex reversal can be induced is from approximately 8 to 98 d after hatching, with a total treatment period of 36 d. This finding contradicts Yamamoto (1969), who stated that hormone treatment should be undertaken when gonads are sexually indifferent and should be continued through the stage of sex differentiation to induce complete and functional sex reversal in fish. The production of sex-reversed male carp solves the problem of hybridization of inbred lines produced by successive gynogenesis. It has several other advantages. The offspring of sex-reversed males mated with normal females are exclusively females. The female unisexual populations are particularly valuable in cases where

TABLE 3. Sex reversal of carp by oral administration of methyltestosterone between various length ranges at 25°C.

Group	L	M	N	O[a]	P[a]	R	S
Treated in length range (mm)	7–21	13–39	19–57	25–75	31–99	37–111	43–129
No. of animals:							
at beginning of treatment	100	80	80	65	52	55	33
at end of treatment	64	56	40	30	23	24	17
tested	10	8	10		26	16	16
Average weight (g):							
at beginning of treatment	0.003	0.03	0.1	0.3	1.7	1.2	2.0
at end of treatment	0.2	1.4	4.5	12.0	22.0	39.3	59.0
Sex distribution among the animals tested in percent:							
female	0	0	0	12.5		12.5	100
male	90	100	90	77		50	0
undifferentiated	10	0	10	23		37.5	0

[a]The groups O and P were intermixed as a result of accidentally misplaced indentification tags.

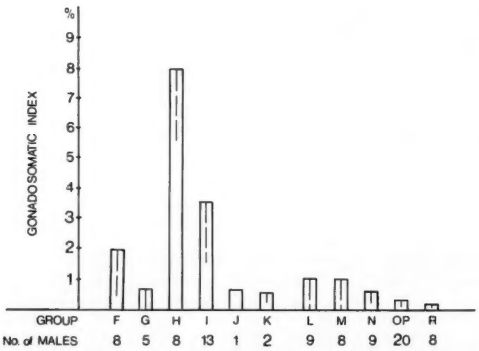

FIG. 1. Effect of oral administration of methyltestosterone on the mean gonadosomatic index of sex-reversed males in the groups treated. Broken lines represent standard deviations.

reproduction is undesirable or must be eliminated, and in commercial breeding because the female carp has a 15% higher growth rate than the male (Wolfarth et al. 1975).

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Comment on Optimum Swimming Speeds in Fish

COMMENT

In a recent paper Trump and Leggett derived an expression for the optimal swimming speed of a migrating fish. To obtain their result they made specific assumptions about the energetic cost of swimming and about the nature of variation in the current, as evidenced by the statement that their solution ". . .is a result of the exponential relationship between energy expenditure and swimming speed [which] applies to situations where currents have periodic oscillations . . ." Since the conclusions of their paper are quite interesting and a valuable contribution to the theory of optimal behavior, it is worth noting that these restrictions are unnecessary and that the result is much more general.

Trump and Leggett assumed that migrating fish seek to minimize the ratio of the energetic cost of migration to the distance traveled. Let $E(W)$ be the energetic cost of swimming at speed W through the water and let $V = W - U$ be the speed made good over the bottom. Then the solution of the variational problem

$$\frac{\delta}{\delta W(t)} \left[\frac{\int_0^T E(W)\, dt}{\int_0^T V\, dt} \right] = 0$$

is

$$\frac{\partial E}{\partial W(t)} = \frac{\int_0^T E(W)\, dt}{\int_0^T (W - U)\, dt}$$

The right-hand side of this equation is independent of t, so the left-hand side must be constant as well. Therefore unless $E(W)$ is a linear function of W or exhibits other unrealistic mathematical behavior, there is a unique constant value of W which satisfies this equation. Using a constant value of W in the equation leads to the solution

$$\frac{W - \overline{U}}{E} \cdot \frac{\partial E}{\partial W} = 1$$

where

$$\overline{U} = \int_0^T U\, dt/T$$

is the mean value of the current.

This result shows quite generally that the optimal strategy of a migrating fish is to maintain a constant speed relative to the water, and this result does not depend on the exponential form for energy expenditure or on the periodic nature of any variation in the current; it does, however, depend on the validity of the assumption that fish seek to minimize energy cost per distance traveled without regard to travel time and related costs, such as exposure to predation. Also, of course, the precise functional form of the relationship between W and $\overline{U}$ depends on the form of $E(W)$ and it is easy to see that $W - \overline{U}$ will be independent of $\overline{U}$ only in the case where $E(W)$ is an exponential function of W. On the other hand, the generality of the conclusion that the optimal swimming speed depends only on the mean current speed $\overline{U}$ and not on its variance suggests a possible limitation of the theory, in that in the presence of strong adverse currents fish are likely to look for a refuge from the current rather than attempting to fight it in an "optimal" manner. — WILLIAM SILVERT, *Department of Fisheries and Oceans, Marine Ecology Laboratory, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S. B2Y 4A2.*

TRUMP, C. L., and W. C. LEGGETT. 1980. Optimum swimming speeds in fish: the problem of currents. Can. J. Fish. Aquat. Sci. 37: 1086–1092.

REPLY

We were pleased to read Dr Silvert's comment on "Optimum Swimming Speeds in Fish: The Problem of Currents" by Trump and Leggett (1980), and thank him for rigorously demonstrating the generality we suspected but did not prove: that any biologically realistic energy relation that increased as a function of swim speed would give results basically similar to those we reported.

Dr Silvert's comment also points out a potentially misleading aspect of our paper. Our model is presented as if the only behavioral response available to a fish in the presence of currents is to adjust its swimming speed to the current regime experienced. Obviously an alternative strategy is to change the effective current regime by altering where it swims. Such an opportunity is clearly open to fish moving upstream in a tidal estuary. Significant energy savings could be achieved by swimming near the bottom during the ebb tide, where the counter current is weakest, and near the surface during flood tide, where the following current is strongest.

Leggett (1976) has demonstrated the potential for such energy-saving behavior by American shad migrating in the Connecticut River, and Brett's (1965) analysis of Idler and Clemens' (1959) estimates of energy expenditure by sockeye salmon suggests that sockeye actively seek out and swim in areas of reduced current during their upriver migration in the Fraser River, B.C.

It must be stressed, however, that the seeking out of reduced currents or refuges in the face of strong adverse currents, as Dr Silvert has proposed, does not negate the model, but rather alters the input parameters. Regardless of the current conditions encountered or selected the optimum solution we describe prevails. — CLIFFORD L. TRUMP, *Department of Biology, Laval University, Quebec, Que. G1K 7P4* AND WILLIAM C. LEGGETT, *Department of Biology, McGill University, Montreal, Que.* H3A 1B1.

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BOOK REVIEWS/COMPTES RENDUS

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Les substances organiques naturelles dissoutes dans l'eau de mer (Colloque du Groupement pout l'Avancement de la Biochimie Marine). *Coordinated by Hubert J. Ceccaldi. Centre National de la Recherche Scientifique, 15, Quai Anatole France, 75700 Paris, France. 1978. iii + 270 p. 85.00 F.*

This publication contains 13 papers presented at a colloquium held at one of the annual meetings of GABIM (a group of biologists, biochemists, chemists, and physiologists with common interests in marine biochemistry, and whose studies are devoted to natural organic substances dissolved in seawater). The focus of such a group was primarily upon substances with known biological activity, but as Professor Maurice Fontaine puts it in his introduction, "are there any organic substances dissolved in seawater which do not exercise, directly or indirectly, biological activity?".

Specific action of individual organic compounds toward particular marine organisms, imperative for successful "information function" of organic compounds in seawater, is emphasized by Fontaine and discussed at length by Aubert (the originator of the useful term "telemediator" for a substance synthesized by marine plants or animals, released to seawater, and acting at a distance upon the behavior or biological functions of the same or other species). Aubert presents, in a systematic way, the results of years of experimentation, but even in his tabulated data, the chemical nature of the telemediator is more often than not listed as unidentified.

It is the task of the chemist to identify dissolved organic matter (DOM) in seawater, as it is of the biologist to investigate its biological functions, and this is done in a number of contributions to this volume. Daumas deals concisely with the chemical nature of "marine humus," the unknown 70% of the dissolved organic matter of seawater which most marine organic chemists continue to ignore. He favors derivations from marine, rather than terrestrial, sources on the basis of chemical, isotopic, and other recent compositional evidence. According to Pelet, in the sole geochemical contribution, the "humic" (alkali-extractable) fraction accounts for up to 50% of marine sedimentary organic matter; the remainder being mainly solvent-insoluble. As he rather maliciously points out, the "lipid" (solvent-extractable) fraction, which has been most extensively studied, accounts for less than 1% of the total sedimentary organic matter — one of the lacunae he recognizes in our knowledge of the organic matter of sediments. Barbier and Saliot review the role of lipids in the marine environment and describe their initial attempts to prepare an inventory of this group of compounds which play their most important role, not within water masses and sediments, but at the air/sea and water/sediment interfaces.

The authors of a paper on the importance of vitamins in the sea (Berland, Bonin, Fiala, and Maestrini) reach the interesting conclusion that production (by algae and bacteria) plus (in the litoral zone) terrigenous inputs exceed the needs of the consumers (principally algae). Thus, these subtances are unlikely to have any influence upon primary productivity, though they may significantly influence secondary interactions.

Most of the papers take the form of reviews of topics, e.g. DOM as a source of N and P for algae (Antia, Berland, Bonin, and Maestrini) and as a factor in the biology of Crustacea (Ceccaldi). However, results of research in progress, e.g. extraction of free fatty acids (Marty and Courtot) and amino acids (Marchelidon), organic exchanges between diatoms and their culture medium (Boutry), the uptake of lipophilic organic compounds (Fevrier), and the absorption of labeled DOM by marine invertebrates (Pavillon) are also presented.

The author of the fore and afterword (Ceccaldi) is too modest when he describes this volume as a synthesis of ideas about an important area of interaction between the biology and the chemistry of the sea, for the use of the francophone scientific community. It is an excellent resource text with no current equivalent in English, and a salutory reminder that the language of Lavoisier is still a legitimate international vehicle for the expression of interesting facts and stimulating ideas in modern marine science.

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Diversity and Adaptation in Fish Behaviour. Zoophysiology Vol. 11. *Miles H. A. Keenleyside. Springer-Verlag, Berlin, Germany. 1979. xiii + 208 p. $37.90.*

The stated purpose of this book is to describe the variety of behavioral strategies that fish use in coping with the problems of finding and ingesting food, avoiding predation, and reproducing. The approach is a selective review of the literature "biased towards a few groups of fish that ethologists have tended to concentrate on." Within this framework it is successful. For each of his functional categories, Keenleyside presents a catalogue of behavioral types, with examples, references, and clear line drawings. This should provide students of fish behavior with a good, though very expensive, introduction to the literature and to the wide range of behavioral variation that fishes demonstrate. However, they will find that diurnal, percoid fishes of coral reefs, temperate lakes, and

home aquaria are over-represented in the coverage.

To many potential readers the title may promise a more comprehensive treatment than the author intended. People interested in habitat selection or behavioral responses to physicochemical variation in the environment will find that Keenleyside has followed traditional ethology in paying scant attention to this area. Responses to fishing gear are ignored in the section on antipredator adaptations. Anyone wishing to use this book to obtain comparative data will be frustrated by the selectivity of the coverage and the lack of quantitative documentation of general trends. "Adaptation" can be used as a post hoc explanation for the diversity of form, or as a scientific hypothesis subject to test. Although this book adopts the former approach, it may lay the groundwork for the latter.

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British Marine Amphipoda: Gammaridea. *Roger J. Lincoln. British Museum (Natural History), London. 1979. 657 p. £ 50.*

Roger Lincoln's impressive new compendium of one of the world's best-studied regional amphipod faunas provides line illustrations, diagnoses, keys, and distributional ecological information on 271 species of gammaridean amphipod crustaceans recorded to date from coastal marine waters (to depths of 200 m) in the British Isles and immediate northeastern Atlantic region. The taxonomic section, comprising about five-sixths of the text, treats the species semiphyletically by family unit, and alphabetically by genus and species within each family. Introductory sections contain useful information on marine census areas of the British Isles, preservation and preparation of specimens, and background and "rationale" for the current status of amphipod systematics. Lists of species according to biogeographic and ecological categories, a selected annotated bibliography, a general bibliography, and a glossary of terms complete the work.

A contribution of this scope and magnitude literally "bursts" with attractive features; perhaps unavoidably it also contains some defects. Thus, readers will appreciate the fresh clean penmanship of the line illustrations, the inclusion of many "whole animal" drawings and their proximity to pertinent text material, and to the keys. On the other hand, the experienced taxonomist may be somewhat disconcerted by the low frequency of illustrations of mouthparts, coxal gills, brood lamellae, pleopods, and telson that often bear characters critical to modern classification and phylogeny. Lincoln's higher classification is basically phyletic. Refreshing is his acceptance of many of the recently proposed higher (family level) concepts within the Gammaroidea and Melitoidea, and the transfer of *Megaluropus* to the melphidippids, *Gammarellus* to the eusirids, and *Cerapus* and *Ericthonius* to the ischyrocerids. Unaccountably, however, he has missed the general acceptance of *Lagunogammarus* Sket 1971 for the *Gammarus oceanicus* group, the previous transfers of *Unciola* and related genera to the aorids (close to *Lembos smithi*) where they belong, the separation of Haustoriidae and Pontoporeiidae, and the creation of Urothoidae (within the Phoxocephaloidea). He has incorrectly placed *I. picta* in the genus *Listriella* instead of creating for it a new genus based on at least five important characters, but realistically has proposed the new genus *Paramphilochoides* to encompass the *intermedius–odontonyx* group of *Amphilochoides*. Regrettably, the author's publication deadline was too early to take advantage of the most recent papers embodying new superfamily concepts and probable phyletic relationships within the Amphipoda; his own classification is thus already outmoded and unlikely to be followed in future.

Lincoln's general taxonomic approach to identification is standard, with relatively few innovations. While emphasizing sexual dimorphism in antennae, eyes, uropods, etc., in some groups lacking amplexing type gnathopods (♂), the author gives relatively short shrift to the taxonomic importance of the buccal mass and mouthparts, gills, brood plates, pleopods, and telson that often provide more useful, sex- and instar-independent and phyletically significant characters. However, Lincoln (and colleague Des Hurley) are pioneering SEM studies of amphipod surface ultrastructure, especially the antennal calceoli, and their use in phyletic classification. These organelles are presumably sensitive to acoustical or vibrational stimuli but are actually found in about 20 amphipod families (including several freshwater Crangonyctoidea) rather than the eight listed. The keys are basically workable and employ multiple-character couplets, but sometimes rely too heavily on gnathopods and sex-dependent characters. The key to families is highly artificial and uses too many indefinite terms such as "feeble" and "characteristic" (some not defined in glossary), but is made functional by the proximity of good outline drawings of representative family members.

Although the text is relatively free of mechanical and nomenclatural oversights, the author has erroneously assigned the land-hopper *Brevitalitrus hortulanus* to the genus *Talitroides*, omitted *Talorchestia brito* from key couplets, recognized only 5 of the 10-plus existing genera of Talitridea, only four of more than 10 primarily fossorial families of Gammaridea, and only one of three described species of *Haustorius*. He might note that males of Melphidippidae are separable from females on differences in eye size and shape, and form of the weakly amplexing gnathopods, in addition to those of antenna 2, and the Pleustidae are separable from the Calliopiidae on at least eight characters of family and superfamily significance, not just (the) "structure of the upper lip." Regional species coverage seems reasonably complete, although the author appears to have overlooked records of *Bogidiella* sp. from off Eddystone Light (Spooner 1960) and of the freshwater species *Gammarus lacustris* and *G. duebeni celticus*; further collecting will undoubtedly yield species recorded in adjacent waters by other authors.

The basis for the biogeographic lists of species is not clear and not in conformity with categories previously recognized in the literature; moreover, the terms "cold-temperate," "warm-temperate," etc., imply a temperature basis (not given), whereas only a simple geographic distribution pattern

is provided. The value and significance of lists of "intertidal" and "domicolous" species might have been enhanced by including recorded depth ranges in the one instance, and substrate types or algal associates in the other. Greater efficiency in the format might have been achieved by selection of a slightly smaller page size, a smaller type size (especially for species diagnoses), by smaller illustrations grouped in tighter patterns, by elimination of figure legends through use of self-explanatory symbols on body parts, and by page continuity of species accounts. Grouping of plates of similar species, opposite and "back-to-back," would have facilitated species comparisons, and facilitated a lighter weight paper. Greater clarity and impact of species distributions might have been achieved by "spot" distribution maps, rather than text records of county and coastal towns, the locations of which are mostly unknown to non-British readers or require much reference work to envisage.

The book was written essentially to enable British biologists and ecologists, especially those involved in studies of environmental contamination, food energy cycles, population dynamics, etc., to identify readily species within this taxonomically difficult crustacean group; hopefully it would also become a standard regional reference work for both the local taxonomic and wider scientific communities. In balance, the book should largely succeed in these objectives. However, more careful attention to primary problems of marketing such voluminous and detailed information would possibly have enhanced the book's usefulness and financial accessibility to both user groups. Dr Lincoln is to be congratulated on this major new identification manual and basic reference work on amphipod biology.

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Books received/Livres reçus[1]

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Predation and Freshwater Communities. *Thomas M. Zaret. Yale University Press, New Haven, Connecticut 06520. 1980. xiv + 187 p. $15.00 U.S.* (Focusing on the role of freshwater fishes and their zooplankton prey, the dominant freshwater predators are identified, their role in freshwater communities are examined, and the immediate and long-term consequences for prey populations are evaluated.

February/février 1981

***Fisheries Management.** *Edited by Robert T. Lackey and Larry A. Nielsen. Halsted Press of John Wiley & Sons Co., New York. 1980. x + 422 p. $34.95 U.S.* (The stated objective of this book is to present a broad discussion of fisheries management for use by students as a textbook and by professionals as a reference.)

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[1]Entries in this list *not* marked by an asterisk are available for review by interested readers for a 3-month period from the time of publication of the list. For information, please write to the Book Review Editor.

[1]Les ouvrages inclus dans cette liste et *non* accompagnés d'un astérisque peuvent être mis à la disposition de lecteurs intéressés qui voudraient en faire l'analyse, et ce, pour une période de 3 mois à compter de la date de parution de la liste. Pour plus de renseignements, veuillez écrire au rédacteur des Comptes rendus.

ANNOUNCEMENTS/AVIS

International Congress of Ecology

The Third International Congress of Ecology will take place in Warsaw, Poland, September 5–11, 1982, under the auspices of the International Association for Ecology (INTECOL), Ecology Section, International Union for Biological Sciences (IUBS), and the Polish Academy of Sciences.

A major theme of the Congress will be "Ecology as a basis for environmental management and human welfare." The Congress will consist of six main plenary sessions with related concurrent sessions and special symposia organized by the INTECOL Working Groups. The topics covered by the plenary sessions will include the following: Processes integrating ecosystems and landscape, Advancements in the understanding of organismal interactions in ecological systems, Restoration and stabilization of environmental quality, Ecological basis of intensifying biological production, Technological impact of man on the environment, Utilisation of ecological expertise in resource management and regional planning. Sessions planned for the INTECOL Working Groups include the following: Statistical ecology, Physiological ecology, Urban ecology, Environmental education, Aquatic ecology, Granivorous birds, Special symposium on "Ecology of polar regions."

Each session will be organized by Conveners appointed by the Steering Committee. Oral contributions, poster presentations, and scientific films will form the main means for active participation. The Official Congress language is English. Registration fees are $100 (U.S.) for participants and $60 (U.S.) for accompanying persons and students. The first announcement outlining details and a preliminary application form are now available. All correspondence and requests for information should be sent airmail to: *Congress Secretariat of III INTECOL Congress, Institute of Ecology, Dziekanów Leśny, 05-150 Lomianki, Poland*, or by *telex 817378 IE PAN PL*.

Congrès international d'écologie

Le troisième Congrès international d'écologie aura lieu à Varsovie (Pologne) du 5 au 11 septembre 1982, sous les auspices de l'Association internationale d'écologie (INTECOL), la section Écologie, Union internationale des sciences biologiques (IUBS) et l'Académie polonaise des sciences.

Le Congrès aura pour thème principal l'« Écologie, fondement de la gestion de l'environnement et du bien-être de l'Homme ». Il y aura six principales séances plénières, avec séances simultanées çonsacrées à des sujets connexes, ainsi que colloques spéciaux organisés par les groupes de travail de l'INTECOL. Parmi les sujets traités en séances plénières, on mentionne : processus intégrant écosystèmes et paysage, progrès dans la compréhension des interactions des organismes dans les systèmes écologiques, restauration et stabilisation de la qualité de l'environnement, fondement écologique d'une production biologique accrue, impact technologique de l'Homme sur l'environnement, utilisation des connaissances écologiques dans la gestion des ressources et la planification régionale. Les séances prévues pour les groupes de travail de l'INTECOL incluent les sujets suivants : écologie statistique, écologie physiologique, écologie urbaine, éducation touchant l'environnement, écologie aquatique, oiseaux granivores, colloque spécial sur l'« écologie des régions polaires ».

Un convocateur, nommé par le comité de direction, organisera chaque séance. Comme principaux moyens de participation active, il y aura contributions verbales, présentations d'affiches et projections de films scientifiques. La langue officielle du Congrès est l'anglais. Les frais d'enregistrement sont de $100 (É.-U.) pour les participants, et de $60 (É.-U) pour les personnes accompagnant des participants et pour les étudiants. On peut se procurer dès maintenant le premier avis contenant les détails, ainsi qu'un formulaire d'application préliminaire. On est prié d'adresser, par courrier aérien, toute correspondance et demande de renseignements à: *Congress Secretariat of III INTEL Congress, Institute of Ecology, Dziekanów Leśny, 05-150 Lomianki, Pologne*, ou par *telex 817378 IE PAN PL*.

Society of Canadian Limnologists (S.C.L.) Formed

The delegates present at the 3rd annual meeting of the Canadian Chapter of the International Society for Theoretical and Applied Limnology (S.I.L.) voted to accept the constitution proposed by Drs T. G. Northcote and F. J. Ward and thus brought into being the Society of Canadian Limnologists (S.C.L.).

The aim of S.C.L., which will be affiliated with S.I.L., is the advancement of all branches of theoretical and applied limnology (physical, chemical, and biological) in Canada, including not only scientific aspects but also better public understanding of the fundamental importance of inland waters to Canada.

The S.C.L. will provide opportunities for limnologists

Création d'une société canadienne de limnologie (S.C.L.)

Les délégués présents à la troisième rencontre annuelle de la section canadienne de la Société internationale de limnologie théorique et appliquée ont accepté la constitution proposée par Dr T. G. Northcote et Dr F. J. Ward, créant ainsi la Société canadienne de limnologie (S.C.L.).

L'objectif de la S.C.L., qui sera affiliée à la S.I.L., est de favoriser l'avancement de toutes les branches de la limnologie appliquée et théorique (physique, chimique, biologique) au Canada; on espère éalement arriver à faire comprendre auc Canadiens l'importance des eaux intérieures.

La S.C.L. fournira aux limnologistes canadiens la possibilité d'échanger des idées et de l'information scientifique lors

throughout Canada to exchange views and scientific information at a regular annual meeting, will initiate regular newsletters, and will encourage special scientific activities. The Society will present to governments and to the general public its views on questions related to the quality of inland aquatic environments, and will arrange and present the views of the membership on matters concerning inland waters at international forums including S.I.L.

Three categories of members exist within the society. These are:

a) International members, i.e. members of both S.I.L. and S.C.L., membership fee — $5.00 and current S.I.L. fee.

b) General members, i.e., members of S.C.L. only, membership fee $10.00.

c) Student members, i.e. members enrolled in undergraduate or graduate programs in Canadian universities, membership fee $5.00.

Membership in the society is open to all persons with an interest in limnology.

For further information please contact until mid-September 1981:

John F. Flannagan, Acting Secretary/Treasurer, Freshwater Institute, 501 University Crescent, Winnipeg, Man. R3T 2N6, and after mid-September 1981: *F. J. Ward, Secretary/Treasurer, Department of Zoology, University of Manitoba, Winnipeg, Man. R3T 2N2.*

d'une assemblée annuelle; en outre, elle publiera un bulletin périodique et encouragera certaines activités scientifiques spéciales. La Société pourra présenter aux gouvernements et au public en général son point de vue sur des questions relatives à la qualité de l'environnement des eaux intérieures, elle recueillera l'opinion de ses membres sur des sujets concernant les eaux intérieures pour les représenter à des réunions internationales, dont celle de la S.I.L.

Il existe trois catégories de membres à l'intérieur de la Société. Ce sont:

a) les membres internationaux, c.-à-d. membres de la S.I.L. et de la S.C.L., cotisation de $5 plus cotisation de la S.I.L.;

b) les membres généraux, c.-à-d. membres de la S.C.L. seulement, cotisation de $10;

c) les membres étudiants, c.-à-d. membres qui font des études de premier ou de deuxième cycle dans les universités canadiennes, cotisation de $5.

Toute personne s'intéressant à la limnologie peut devenir membre de la Société.

Pour obtenir des renseignements supplémentaires, veuillez communiquer avec les personnes suivantes: d'ici la mi-septembre 1981:

John F. Flannagan, Secrétaire-trésorier suppléant, Institut des eaux douces, 501, University Crescent, Winnipeg (Man.) R3T 2N6 et à compter de la mi-septembre 1981: *F. J. Ward, Secrétaire-trésorier, Département de zoologie, Université du Manitoba, Winnipeg (Man.) R3T 2N2*

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Growth patterns in sand lance, *Ammodytes dubius*, from the Grand Bank **G. H. Winters**

Some toxic constituents of chlorination-stage effluents from bleached kraft pulp mills **A. B. McKague**

Salmon stock identification using a microanalytic technique to measure elements present in the freshwater growth region of scales **L. A. Lapi and T. J. Mulligan**

Comparison of ozone and chlorine toxicity to the developmental stages of striped bass, *Morone saxatilis* **L. W. Hall Jr., D. T. Burton, and L. B. Richardson**

Advanced photoperiod and water temperature effects on gill Na^+-K^+ adenosine triphosphatase activity and migration of juvenile steelhead (*Salmo gairdneri*) **W. S. Zaugg**

The first diets of postemergent brook trout (*Salvelinus fontinalis*) and atlantic salmon (*Salmo salar*) alevins in a Quebec river **D. D. Williams**

Which witch is which? A study of the stock structure of witch flounder (*Glyptocephalus cynoglossus*) in the Newfoundland region **D. J. Fairbairn**

Avoidance reactions of juvenile coho salmon (*Oncorhynchus kisutch*) to monocyclic aromatics **D. J. Maynard and D. D. Weber**

Avoidance reactions of migrating adult salmon to petroleum hydrocarbons **D. D. Weber, D. J. Maynard, W. D. Gronlund, and V. Konchin**

A probability transition matrix model for yield estimation in fisheries with highly variable recruitment **W. M. Getz and G. L. Swartzman**

Temporal intra-population differences in energy allocation and use by American shad (*Alosa sapidissima*) during the spawning migration **B. D. Glebe and W. C. Leggett**

Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences **B. D. Glebe and W. C. Leggett**

Deep-water eelpouts, Zoarcidae, from Arctic Canada and Alaska **D. E. McAllister, M. E. Anderson, and J. G. Hunter**

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Extracellular secondary metabolite production by the marine dinoflagellate *Prorocentrum minimum* in culture **C. G. Trick, P. J. Harrison, and R. J. Andersen**

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